

Phylogeny of the Family Platycephalidae and Related Taxa (Pisces: Scorpaeniformes)

Hisashi Imamura

Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, 3-1-1
Minato-cho, Hakodate, Hokkaido 041, Japan

(Received 1 September 1996; Accepted 9 December 1996)

The phylogenetic relationships of Platycephalidae and its related taxa were analyzed. Platycephaloidei and Scorpaenoidei form a monophyletic group supported by two synapomorphies: presence of a backwardly-directed opercular spine and an extrinsic muscle derived from the hypaxial. Platycephaloidei and *Plectrogenium*, the triglids and peristediids are monophyletic, characterized by a posterior pelvic fossa. *Bembradium* and *Plectrogenium* constitute a monophyletic group, which divided initially from remainder of the clade. Next *Parabembras*, followed by *Bembras*, branched off the latter. Platycephalidae and its sister group, including the triglids, peristediids and hoplichthyids, have 4 synapomorphies. The triglids, peristediids and hoplichthyids share 15 apomorphies. The peristediids and hoplichthyids constitute a monophyletic group supported by 8 synapomorphies. The newly-defined suborder Platycephaloidei includes the following 7 families: Plectrogeniidae, Parabembridae, Bembridae, Triglidae, Peristediidae, Hoplichthyidae and Platycephalidae. Platycephalidae is redefined, being a monophyletic group supported by 6 synapomorphies, and including 2 subfamilies and 17 genera, 3 of them new.

Key words: Phylogeny, Platycephalidae, Platycephaloidei, monophyly, cladistic classification, *Eurycephalus* gen. nov., *Solitas* gen. nov., *Ambiserrula* gen. nov.

Introduction

The family Platycephalidae (*sensu* Nelson 1994) consists of 14 genera and about 58 species (Keenan 1991) that inhabit nearshore bottoms (usually 1-200m depth) of tropical and temperate seas. They are predominantly Indo-Pacific in distribution, with two species entering eastern Atlantic (*Grammoplites gruvelli* (Pellegrin, 1905)) and eastern Mediterranean (*Platycephalus indicus* (Linnaeus, 1758)) waters (Knapp 1981, 1984, 1986; Hureau 1986).

Platycephalid systematics have been studied by many ichthyologists. Jordan and Richardson (1908) classified Japanese platycephalids into four genera, but did not recognize subfamilies. Jordan and Hubbs (1925) later recognized four subfamilies, Onigociinae, Rogadiinae, Inegociinae and Platycephalinae, in the Platycephalidae and assigned *Parabembras* and *Bembras* to the families Parabembridae and Bembridae, respectively. Whitley (1931a) separated Platycephalidae into six subfamilies, Rogadiinae, Onigociinae, Inegociinae, Elatinae, Thysanophryinae and Platycephalinae, and Fowler (1938) established two further subfamilies, Grammoplitinae and Cymbacephalinae. Matsubara and Ochiai (1955), however, recognized only four subfamilies, Onigociinae, Inegociinae, Elatinae and Platycephalinae, in Platycephalidae, which Matsubara (1955) placed in the superfamily Platycephalicae

Current address: Hachinohe Branch, Tohoku National Fisheries Research Institute,
25-259 Same, Hachinohe, Aomori 031, Japan

(=Platycephaloidea) along with Parabembridae, Bembridae and Hoplichthyidae. Although Nelson (1976, 1984) recognized only two subfamilies, Platycephalinae and Bembradinae, the latter including *Bembras*, *Parabembras*, *Bembradium* and *Bembradon*, Keenan (1991) separated the Australian platycephalids into Cymbacephalinae, Onigociinae, Inegociinae, Elatinae and Platycephalinae. On the other hand, Nakabo (1993) did not recognize any platycephalid subfamilies. Furthermore, because he considered *Bembradon* to resemble members of the percophid *Bembrops*, he did not include *Bembradon* in his Platycephalidae. Recently Nelson (1994) separated his earlier (1976, 1984) Platycephalidae into two families, Platycephalidae and Bembridae, and Imamura and Knapp (1997) followed Nelson's (1994) definition. The limits of some genera in the Platycephalidae are as unclear as those of the subfamilies, the dearth of knowledge surrounding platycephalid phylogeny having contributed to the numerous conflicts. The phylogenetic relationships of the group have been studied by Matsubara and Ochiai (1955) and Keenan (1991). The former examined only 10 Japanese species and proposed family relationships based on limited osteological data. Keenan (1991) constructed the relationships of 24 Australian species in 11 genera, using allozyme analysis. However, both of these studies relied on materials collected from limited areas. A comprehensive phylogenetic study using a wide range of materials is clearly needed.

The goals of this study were: (1) to determine the evidence supporting the monophyly of Platycephalidae; (2) to clarify the interrelationships of Platycephalidae; and (3) to propose a classification of the families, subfamilies and genera in the suborder Platycephaloidei based on their phylogeny.

Materials and Methods

Materials used for anatomical examinations in this study are listed below. Institutional abbreviations follow Leviton *et al.* (1985). Osteological examinations were made on specimens stained in Alizarin Red-S, and a Nikon AMZ-10 and Wild M-8 with a camera lucida were used when making drawings. Counts and proportional measurements of external features follow Hubbs and Lagler (1958). Specimen lengths are expressed as standard length (SL). Measurements were made with calipers to the nearest 0.1 mm. Terminology generally follows Yabe (1985) for osteology and Winterbottom (1974) for myology, except for the swimbladder muscles, the terminology of which follows Hallacher (1974). Definitions of higher taxonomic categories in the material list follow Nelson (1994), except those of Triglidae and Peristediidae, which follow Matsubara (1955), and Hexagrammoidei and Zaniolepidoidi, which follow Shinohara (1994). The initial generic positions of platycephalid species followed recent works (e. g. Knapp 1979, 1981, 1984, 1986, 1987, 1991, 1992; Knapp and Wongratana 1987; Paxton *et al.* 1989; Keenan 1991; Imamura and Amaoka 1994; Imamura *et al.* 1995).

Materials used for dissection

Scorpaeniformes

Platycephaloidei

Platycephalidae. *Cociella crocodila* (Tilesius, 1812), HUMZ 35250 (248mm); *Cymbacephalus beauforti* (Knapp, 1973), HUMZ 135113 (393mm); *C. nematoph-*

thalmus (Günther, 1860), FSFL P474 (284mm); *C. staigeri* (Castelnau, 1875), NTM S.13718-016 (ca. 330mm); *Elates ransonneti* (Steindachner, 1877), HUMZ 112076 (123mm); *Grammoplites gruveli* (Pellegrin, 1905), BMNH 1914.2.2 (119mm); *G. portuguesus* (Smith, 1953), HUMZ 135110 (128mm); *G. scaber* (Linnaeus, 1758), FUMT-P (unregistered, 139mm); *G. suppositus* (Troschel, 1840), HUMZ 135123 (172mm); *Inegocia japonica* (Tilesius, 1812), HUMZ 5204 (226mm); *Neoplatycephalus conatus* (Waite and McCulloch, 1915), AMS E.3472, NMV A.2916 (2, 285-381mm); *N. richardsoni* (Castelnau, 1872), AMS IB.7601 (263mm); *Onigocia macrolepis* (Bleeker, 1854), HUMZ 49467 (96mm); *O. spinosa* (Temminck and Schlegel, 1842), HUMZ 49442 (81mm); *Papilloculiceps longiceps* (Ehrenberg, 1829), HUMZ 113412 (149mm); *Platycephalus bassensis* Cuvier, 1829, AMS I.12795 (192mm); *P. caeruleopunctatus* McCulloch, 1922, AMS E.1783 (336mm); *P. fuscus* Cuvier, 1829, AMS I.30344-001 (210mm); *P. longispinis* Cuvier, 1829, AMS 24802-001 (140mm); *P. marmoratus* Stead, 1908, AMS I.20870-001 (152mm); *Ratabulus diversidens* (McCulloch, 1914), AMS I.25897-007 (140mm); *R. megacephalus* (Tanaka, 1917), HUMZ 39705, 39720 (2, 189-204mm); *Rogadius asper* (Cuvier, 1829), HUMZ 48678, 49465 (2, 137-139mm); *R. patriciae* Knapp, 1987, HUMZ 135135 (139mm); *R. pristiger* (Cuvier, 1829), HUMZ 131415 (110mm); *Sorsogona nigripinna* (Regan, 1905), HUMZ 135132 (163mm); *S. prionota* (Sauvage, 1873), HUMZ 135130 (160mm); *S. tuberculata* (Cuvier, 1829), HUMZ 112104, 112115 (2, 85-102mm); *Suggrundus cooperi* (Regan, 1908), HUMZ 135109 (169mm); *S. jugosus* (McCulloch, 1914), AMS I.20845-001 (125mm); *S. macracanthus* (Bleeker, 1869), AMS I.20906-013 (138mm); *S. meerdervoortii* (Bleeker, 1860), HUMZ 49259, 52607, 63696, 90253 (4, 141-169mm); *S. rodericensis* (Cuvier, 1829), HUMZ 13890, 114964 (2, 108-195mm); *Thysanophrys armata* (Fowler, 1938), HUMZ 135112 (121mm); *T. arenicola* Schultz, 1966, WAM P.28538-013 (131mm); *T. chiltonae* Schultz, 1966, RUSI 15342 (72mm), FSKU (unregistered, 158mm); *T. cirronasa* (Richardson, 1848), AMS I. 25450-001 (219mm); *T. otaitensis* (Parkinson, 1829), WAM P.27824-080 (89mm).

Bembridae. *Bembradium roseum* Gilbert, 1905, HUMZ 75105, 79190 (2, 85-133mm); *Bembras japonica* Cuvier, 1829, HUMZ 49409, 49411, 49412 (3, 160-182mm); *Parabembras curta* (Temminck and Schlegel, 1842), HUMZ 108335, 108460, 108778 (3, 135-165mm).

Hoplichthyidae. *Hoplichthys gilberti* Jordan and Richardson, 1908, HUMZ 51736 (152mm); *H. haswelli* McCulloch, 1907, HUMZ 50268 (341mm); *H. langsfordii* Cuvier, 1829, HUMZ 75337 (156mm).

Scorpaenoidei

Scorpaenidae. *Adelosebastes latens* Eschmeyer, Abe and Nakano, 1979, HUMZ 72035 (206mm); *Apistus carinatus* (Bloch, 1801), HUMZ 37372 (93mm); *Dendrochirus zebra* (Quoy and Gaimard, 1824), HUMZ 63987 (132mm); *Helicolenus hilgendorfi* (Steindachner and Döderlein, 1884), HUMZ 39743 (136mm); *Hozukius guyotensis* Barsukov and Fedrov, 1975, HUMZ 71936 (232mm); *Hypodytes rubripinnis* (Temminck and Schlegel, 1843), HUMZ 35880 (70mm); *Inimicus japonicus* (Cuvier, 1829), HUMZ 140587 (143mm); *Minous monodactylus* (Bloch and Schneider, 1801), HUMZ 101864 (95mm); *Neosebastes thetidis* (Waite, 1899), HUMZ 21124 (196mm); *Plectrogenium nanum* Gilbert, 1905, HUMZ 37337 (52mm); *Pontinus macrocephalus* (Sauvage, 1882), HUMZ 99503 (121mm); *Scorpaena izensis* Jordan and Starks, 1904, HUMZ 79974 (134mm); *Scorpaenodes littoralis* (Tanaka, 1917), HUMZ 101394 (74mm); *Scorpaenopsis neglecta* Heckel, 1837, HUMZ (unregistered, 125mm);

Sebastes owstoni (Jordan and Thompson, 1914), HUMZ 42641 (183mm); *Sebastolobus macrochir* (Günther, 1880), HUMZ 59268 (112mm); *Sebastiscus marmoratus* (Cuvier, 1829), HUMZ 69895 (125mm); *Setarches longimanus* (Alcock, 1894), HUMZ 79505 (125mm); *Trachyscorpia capensis* (Gilchrist and von Bonde, 1924), NSMT-P 41332 (235mm).

Aploactinidae. *Erisphex potti* (Steindachner, 1896), HUMZ 108774 (87mm).

Triglidae. *Bellator egretta* (Goode and Bean, 1896), HUMZ 69393 (81mm); *Chelidonichthys spinosus* (McClelland, 1844), HUMZ 108541 (200mm); *Lepidotrigla microptera* Günther, 1873, HUMZ 48942 (159mm); *Prionotus stearnsii* Jordan and Swain, 1884, HUMZ 32456 (98mm); *Pterygotrigla macrorhynchus* Kamohara, 1936, HUMZ (unregistered, 95mm).

Peristediidae. *Peristedion orientale* Temminck and Schlegel, 1843, HUMZ 106621 (152mm); *Satyrichthys serrulatus* (Alcock, 1898), HUMZ 79844 (227mm).

Anoplopomatoidei

Anoplopomatidae. *Anoplopoma fimbria* (Pallas, 1811), HUMZ 130803 (240mm); *Erilepis zonifer* (Lockington, 1880), HUMZ 88050 (240mm).

Zaniolepidoidae

Zaniolepididae. *Oxylebius pictus* Gill, 1862, BCPM 974-485 (dissected by G. Shinohara, 149mm).

Hexagrammoidei

Hexagrammidae. *Hexagrammos lagocephalus* (Pallas, 1810), HUMZ 104878 (152mm).

Perciformes

Percoidei

Apogonidae. *Apogon semilineatus* Schlegel, 1843, HUMZ 39473 (82mm).

Lethrinidae. *Lethrinus rubrioperculatus* Sato, 1978, HUMZ 113329 (141mm).

Percichthyidae. *Acropoma japonicum* Günther, 1859, HUMZ 39772 (106mm); *Malakichthys wakiyae* Jordan and Hubbs, 1925, HUMZ 39072 (96mm).

Pempheridae. *Pempheris schwenkii* Bleeker, 1855, HUMZ 119435 (115mm).

Serranidae. *Chelidoperca hirundinacea* (Valenciennes, 1831), HUMZ 36481 (102mm); *Diploprion bifasciatum* Kuhl and van Hasselt, 1828, HUMZ 87031 (122mm); *Epinephelus awoara* (Temminck and Schlegel, 1843), HUMZ 97035 (125mm); *Nippon spinosus* Cuvier, 1829, HUMZ (unregistered, 126mm); *Plectranthias kelloggi azumonus* (Jordan and Richardson, 1910), HUMZ 79389 (104mm).

Terapontidae. *Palates quadrilineatus* (Bloch, 1790), HUMZ 122221 (114mm).

Anatomical abbreviations. The following abbreviations are used in the Figures.

Bones and cartilages

ACP, ascending process of premaxillary; ACT, actinost; ALP, alveolar process; ANG, anguloarticular; ARP, articular process; BB, basibranchial; BH, basihyal; BO, basioccipital; BR, branchiostegal ray; BS, basisphenoid; CB, ceratobranchial; CC, cranial condyle; CH, ceratohyal; CLE, cleithrum; COM, coronomeckelian; COR, coracoid; DEN, dentary; DHH, dorsal hypohyal; DP, distal pterygiophore; ECP, ectopterygoid; EB, epibranchial; EH, epihyal; ENP, entopterygoid; EO, exoccipital; EP, epiotic; EPR, epipleural rib; ETH, ethmoid; EU, epural; FRO, frontal; HB, hypobranchial; HH, hypohyal; HS, hemal spine; HYO, hyomandibular; HYP, hypural; IAC, interarcual cartilage; IC, intercalar; IH, interhyal; IO, infraorbital; IOP,

interopercle; LAC, lachrymal; LET, lateral ethmoid; LP, lateral process of maxilla; MAX, maxillary; MEC, meckelian cartilage; MEP, metapterygoid; NS, neural spine; OP, opercle; PA, parietal; PAL, palatine; PB, pharyngobranchial; PC, premaxillary condyle; PEL, pelvis; PHY, parhypural; PMP, postmaxillary process; POP, preopercle; PP, proximal pterygiophore; PR, pleural rib; PRM, premaxillary; PRO, prootic; PS, parasphenoid; PT, posttemporal; PTO, pterotic; PTS, pterosphenoid; PU, preural centrum; PV, prevomer; QUA, quadrate; R, ray; RC, rostral cartilage; RET, retroarticular; S, spine; SCA, scapula; SCL, supracleithrum; SO, supraoccipital; SOP, subopercle; SPO, sphenotic; ST, supratemporal; STA, stay; SYM, symplectic; UN, uroneural; URO, urohyal; US, urostyle; VHH, ventral hypohyal.

Muscles and ligaments

A1-3 and Aw, adductor mandibular sections 1-3 and w; AAP, adductor arcus palatini; ABP, abductor profundus; ABPP, abductor profundus pelvici; ABS, abductor superficialis; ABSP, abductor superficialis pelvici; AD, adductor; ADP, adductor profundus; ADPP, adductor profundus pelvici; ADS, adductor superficialis; ADSP, adductor superficialis pelvici; AH, adductor hyomandibulae; AO, adductor operculi; ARD, arrector dorsalis; ARDP, arrector dorsalis pelvici; ARV, arrector ventralis; ARVP, arrector ventralis pelvici; BL, Baudelot's ligament; CO, coracoradialis; DO, dilatator operculi; EPAX, epaxialis; EXP, extensor proprius; EXT, extrinsic muscle; FD, flexor dorsalis; FDS, flexor dorsalis superior; FV, flexor ventralis; FVE, flexor ventralis externus; FVI, flexor ventralis internus; HAB 1-2, hyohyoidei abductores section 1-2; HAD, hyohyoidei adductores; HIF, hyohyoidei inferioris; HPAX, hypaxialis; HL, hypochordal longitudinalis; IM, intermandibularis; INT, interraddialis; LAP, levator arcus palatini; LE, levator externus; LEP, levator pectoralis; LI, levator internus; LO, levator operculi; LP, ligamentum primordium; OBP, obliquus posterior; OBS, obliquus superioris; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; PH, protractor hyoidei; PP, protractor posterior; RC, rectus communis; RD, retractor dorsalis; RV, retractor ventralis; SO, sphincter oesophagi; STH, sternohyoideus; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior; TVA, transversus ventralis anterior; TVP, transversus ventralis posterior.

Systematic procedure

The cladistic methodology formulated by Hennig (1966) was adopted for estimating the phylogenetic relationships of Platycephalidae and related taxa in this study. Outgroup comparisons (Watrous and Wheeler 1981; Wiley 1981) employing the two-step procedure proposed by Maddison *et al.* (1984) were used to determine character polarity. In the first-step, to define the Platycephalidae and determine its outgroup(s), both Platycephaloidei and Scorpaenoidei (*sensu* Nelson 1994) were analyzed, because the scorpaenoids have been considered closely related to Platycephaloidei (Matsubara 1943, 1955; Matsubara and Ochiai 1955; Washington *et al.* 1984). The other scorpaeniform fishes, i.e. Anoplopomatoidei, Zaniolepidioidei, Hexagrammoidei and Cottoidei (*sensu* Shinohara 1994), were not acceptable for the first-step analysis because of the possibility of a polyphyletic origin of Scorpaeniformes, such having been pointed out by several authors (Quast 1965; Wash-

ington *et al.* 1984; Ishida 1994; Nelson 1994).

Many authors have considered that "scorpaeniforms" were derived from a generalized perciform ancestor (Gill 1888; Regan 1913; Matsubara 1943; Gregory 1933; Lauder and Liem 1983; Johnson and Patterson 1993; Ishida 1994), whereas others (Greenwood *et al.* 1966; Nelson 1994) have suggested that the Scorpaeniformes represent a pre-perciform derivation. Johnson and Patterson (1993) pointed out that Greenwood *et al.* (1966) provided no characters justifying a pre-perciform position for Scorpaeniformes. Nelson (1994) similarly failed to provide supporting evidence and none could be found in this study. Moreover, most characters in scorpaenoids and generalized perciforms have many similarities and are very comparable, as pointed out by Ishida (1994). In this study, the percoids, which have been considered as the primitive group in Perciformes, were employed as the outgroup, their characters generally being taken as the primitive conditions for Platycephaloidei and Scorpaenoidei.

The data was analyzed by using PAUP 3.0s (Swofford 1991), including ACCTRAN (accelerated transformation) optimization and heuristic search opinion. Character evolution was assumed as "ordered" (Wagner parsimony; Farris [1970]), or "unordered" (Fitch parsimony; Fitch [1971]) when a transformation series contained a derived "loss" or it was difficult to order characters because of their many modifications.

Phylogenetic relationships of Platycephaloidei and Scorpaenoidei

Monophyly of Platycephaloidei and Scorpaenoidei, and their relationships.

The relationships of the suborders Platycephaloidei and Scorpaenoidei have been discussed by several authors. Using precladistic methodology, Matsubara (1943, 1955) and Matsubara and Ochiai (1955) considered Platycephaloidei to be related to the scorpaenoid *Plectrogenium*, because they have a more or less depressed head and body, and a series of prominent spines on the sides of the head. However, judgement of the degree of head and body depression is subjective, and the platycephaloids *Thysanophrys cirronasa*, *Platycephalus* and *Neoplatycephalus* lack prominent suborbital spines (Fig. 12A). Furthermore, such spines are usually present in scorpaenoids and cannot be a synapomorphy of Platycephaloidei and *Plectrogenium*. Washington *et al.* (1984) followed Matsubara and Ochiai (1955) because *Parabembras* resembles *Plectrogenium* in having five hypurals and large body scales. However, percoids usually have five hypurals (e. g. Nursall 1963; Fraser 1968; Tominaga 1968; Sasaki 1989; pers. obs.), such being regarded as a plesiomorphic character. Body scale sizes vary among percoids, being "large" (e. g. *Acropoma*, *Malakichthys* and *Plectranthias*) or "small" (e. g. *Epinephelus*, *Nippon* and *Palates*), and polarity is uncertain. Although all species of platycephaloidei and Scorpaenoidei have a well-developed suborbital stay, this characteristic is also seen in other scorpaeniform fishes.

All platycephaloids and scorpaenoids examined, except *Dendrochirus*, have a backwardly-directed opercular spine that extends cross the subopercle (Fig. 1). This spine has not been reported in other scorpaeniforms (Yabe 1985, 1991; Kido 1988; Kanayama 1991; Shinohara 1994; Yabe and Uyeno 1996; pers. obs.). Although the spine is absent in Pteroinae, as figured by Matsubara (1955), a larval specimen (11.5

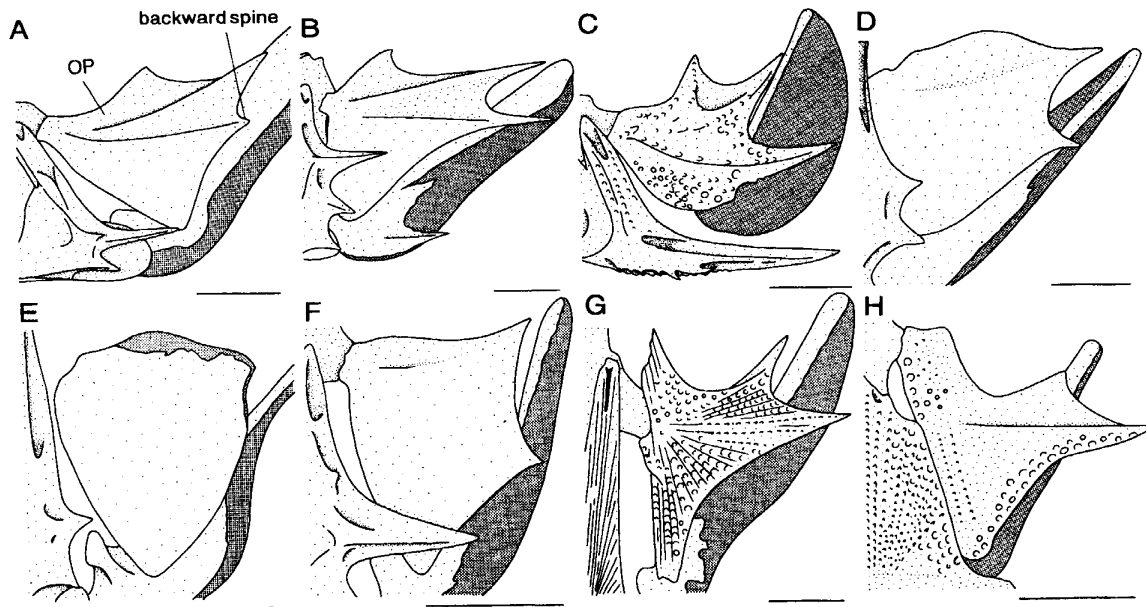


Fig. 1. Lateral aspects of opercle. A, *Grammoplites scaber*; B, *Bembras japonica*; C, *Hoplichthys langsdorfii*; D, *Sebastiscus marmoratus*; E, *Dendrochirus zebra*; F, *Erisphex potti*; G, *Chelidonichthys spinosus*; H, *Peristedion orientale*. Scales indicate 5mm.

mm SL) of *D. zebra* was found to have it (Kojima 1988). Moreover, Imamura and Yabe (1996) described the spine (lower opercular spine *sensu* Moser and Ahlstrom 1978) in a larval specimen (11.0 mm SL) of *Pterois volitans* (Linnaeus, 1758). Accordingly, the absence of this spine in adult Pteroinae is regarded as a secondary reduction. On the other hand, the spine is a rare character in the percoids, being found only in Serranidae (Johnson 1983; pers. obs.) and the epigonid genus *Sphyraenops* (Johnson 1983). Accordingly, presence of the spine is recognized as an apomorphic character defining Platycephaloidei and Scorpaenoidei, which are here regarded as a monophyletic group within the order Scorpaeniformes.

Apomorphic characters in 73 transformation series were considered for the analysis of the relationships within the monophyletic group Platycephaloidei + Scorpaenoidei. The transformation series for these characters are listed and discussed in Appendix 1 and their distribution among the examined taxa is given in Appendix 2. In the first-step analysis, Platycephalidae (*sensu* Nelson 1994) was treated as a single unit. In the case where two or more characters occurred in a transformation series in this family, the most primitive character was accepted as representing the node for Platycephalidae. The interrelationships of the scorpaeniform species were reconstructed on the basis of 36 equally parsimonious trees (Figs 2-4). The consistency index was 0.518 and tree length 166. Characters labelled "r" indicate reversals.

Following the first-step analysis, one character, presence of an extrinsic swimbladder muscle derived from the obliquus superioris, was also regarded as synapomorphic for these suborders (absence of the muscle in some triglids was recognized as a reversal as a result of the analysis). Sasaki (1989) and Shinohara (1994) considered the presence of the extrinsic muscle as a synapomorphy of Scorpaeniformes. However, the muscles of the platycephaloids and scorpaenoids originate from the posteroventral border of the neurocranium, which is the origin of

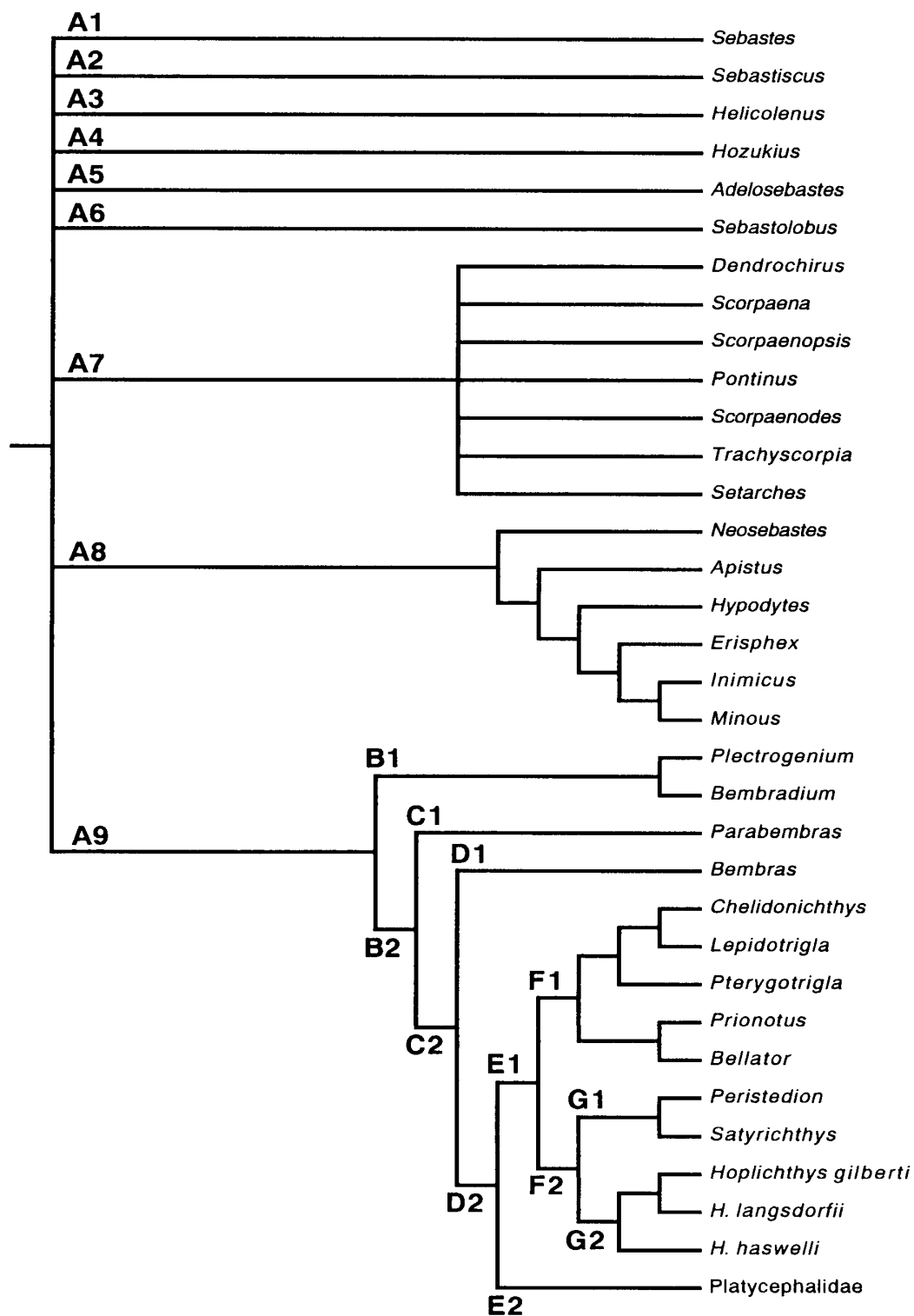


Fig. 2. Strict consensus tree of 36 equally parsimonious cladograms of Platycephaloidei and Scorpaenoidei.

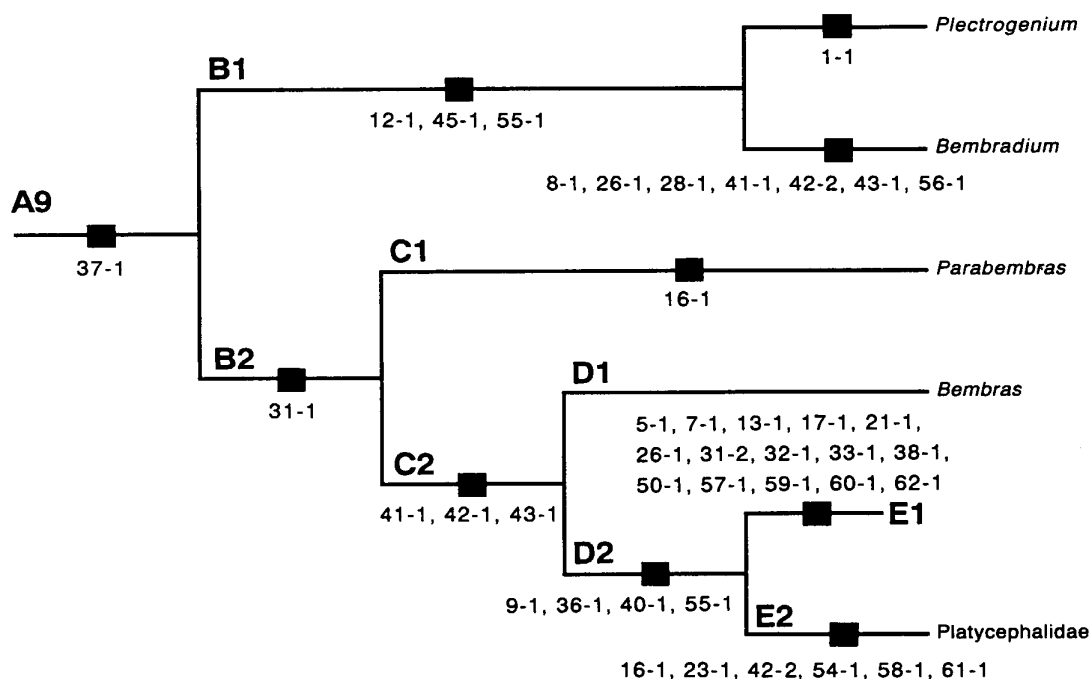


Fig. 3. Phylogenetic relationships of Platycephalidae and related taxa. Numbers of transformation series correspond to those in Appendix 1.

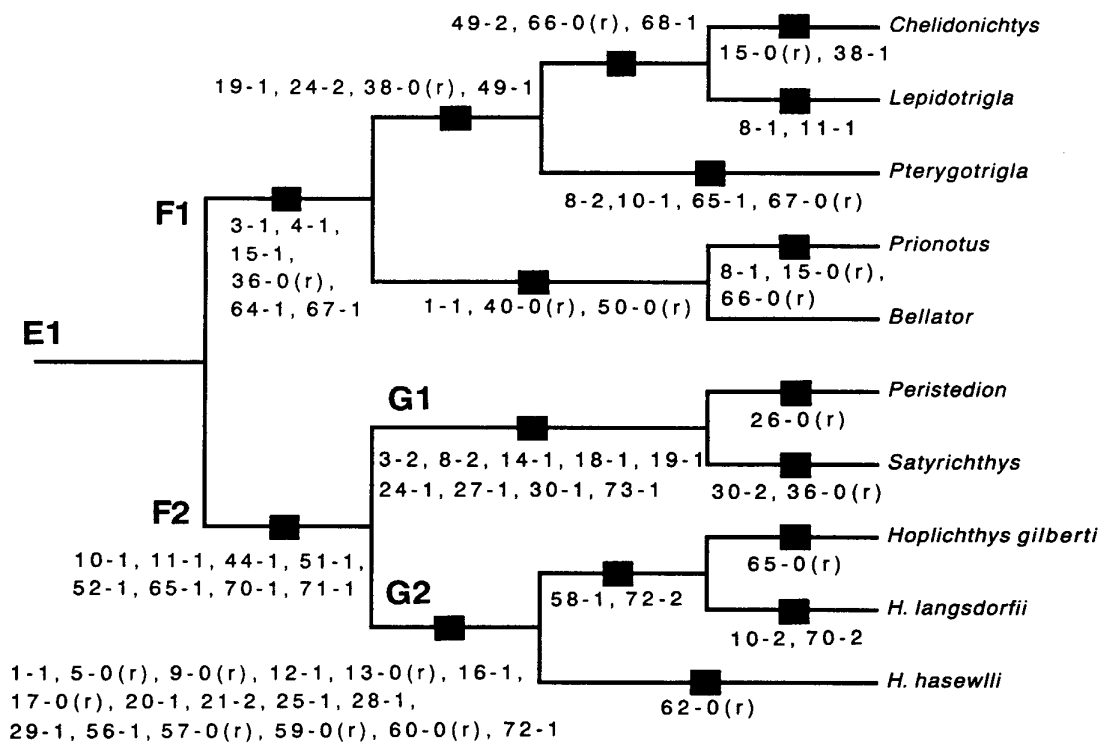


Fig. 4. Phylogenetic relationships of the sister group of Platycephalidae, including Triglidae, Peristediidae and Hoplichthyidae. Numbers of transformation series correspond to those in Appendix 1.

the obliquus superioris in the percoids (pers. obs). The direction of the extrinsic muscle fiber is similar to the obliquus superioris in some scorpaenids. Accordingly, the extrinsic muscles in the platycephaloids and scorpaenoids are considered to have been derived from the hypaxial obliquus superioris. On the other hand, the muscles of other scorpaeniforms, except cottoids (i. e. anoplopomatoids, zaniolepidoids and hexagrammoids), originate mainly from the posttemporal fossa of the neurocranium, which is the origin of the epaxial musculature in the percoids (pers. obs.). Furthermore, these muscles are not well differentiated, it being very difficult to clearly separate the extrinsic muscle from the epaxial, especially in *Anoplopoma fimbria*. Yabe (1985) described the muscle in cottoids as originating from the posteroventral surface of the otolith chamber of the neurocranium and being inserted onto the anterodorsal process of the cleithrum. Based on considerations of parsimony and Shinohara (1994), the cottoid condition can be regarded as an apomorphic character derived from the condition found in anoplopomatoids, zaniolepidoids and hexagrammoids. Therefore, the extrinsic muscle in these four suborders is considered to have been derived from the epaxialis. Accordingly, it is concluded that the extrinsic muscle seen in the Platycephaloidei and Scorpaenoidei is not homologous with that seen in other scorpaeniforms.

Interrelationships in "Platycephaloidei." The monophyletic group comprising Platycephaloidei (*sensu* Nelson 1994) and Scorpaenoidei has nine clades, A1 to A9 (Fig. 2). All Platycephaloidei, Triglidae, Peristediidae and *Plectrogenium* are included in clade A9. On the basis of the relationships established, the suborder Platycephaloidei is redefined to include all members of clade A9. All have a posterior pelvic fossa (Fig. 5). Other scorpaenoids are excluded from the redefined suborder, since they lack the fossa and are regarded as synplesiomorphic with respect to that character.

On the basis of the interrelationships of the newly-defined Platycephaloidei, the family Platycephalidae is also redefined here, being considered a monophyletic group in clade E2 (exclusive of Triglidae, Peristediidae, Hoplichthyidae, *Parabembras*, *Bembras*, *Bembradium* and *Plectrogenium*) (Figs 2, 3), which is supported by six derived characters listed below. This definition of Platycephalidae agrees closely with that of Matsubara (1955) and Nelson (1994).

Clade A9 and its subclades are characterized as follows.

Clade A9. This clade includes all platycephaloids. It is supported by one autapomorphic character, the presence of a posterior pelvic fossa (37-1) (see Appendix) (Fig. 5), a character not found in other scorpaenoids. This clade has two clades, B1 and B2.

Clade B1. In this clade, *Plectrogenium* and *Bembradium* form a monophyletic group, supported by the absence of a sensory canal between the pterotic and preopercle (12-1), presence of a cartilaginous stay (45-1) and the transversus dorsalis anterior being unbranched (55-1) (Fig. 6B).

Within this clade, *Plectrogenium* has the fifth infraorbital fused to the sphenotic (1-1) and *Bembradium* is characterized by the presence of two tooth plates on the prevomer (8-1), absence of an interarcual cartilage (26-1) (Fig. 7C), the first pharyngobranchial being cartilaginous (28-1) (Fig. 7C), absence of the first spine on the first anal fin proximal pterygiophore (41-1), absence of a second element on the first anal fin proximal pterygiophore (42-2), a soft ray on the second anal fin proximal pterygiophore (43-1) and absence of the levator posterior (56-1) (Fig. 6B).

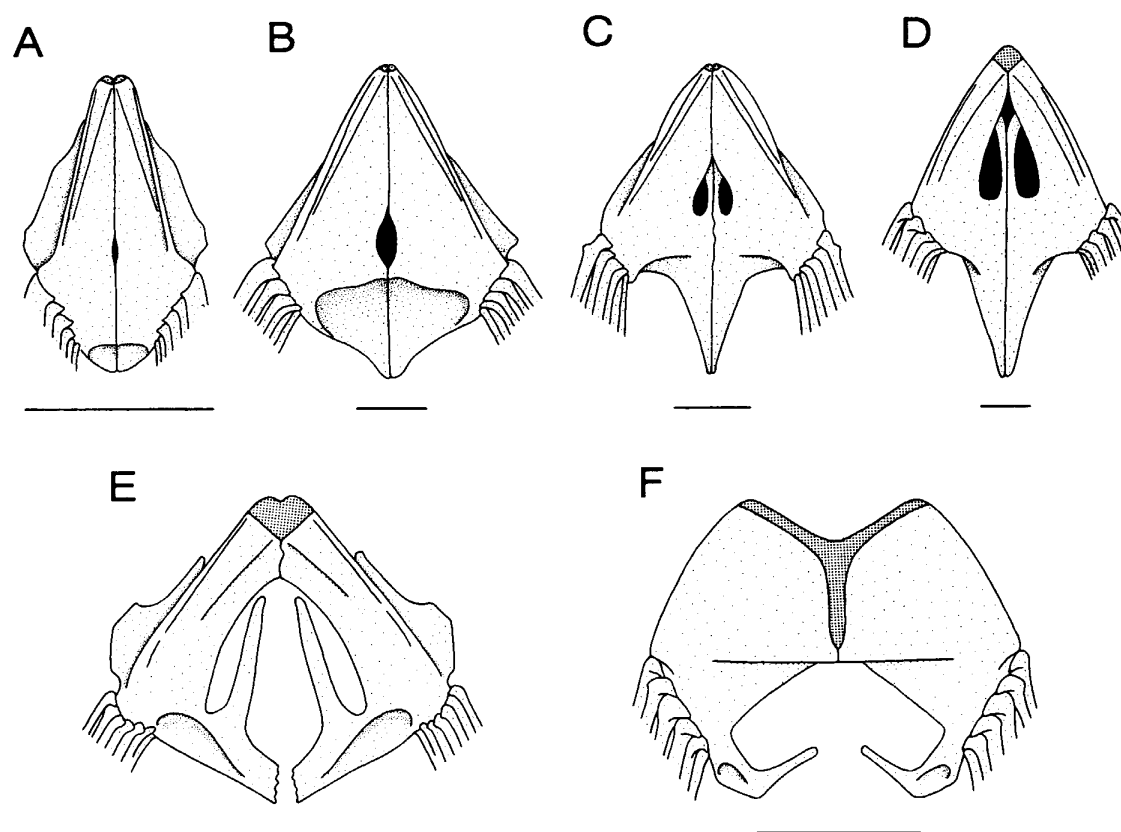


Fig. 5. Pelvis of six species related to Platycephalidae. A, *Plectrogenium nanum*; B, *Parabembras curta*; C, *Bembras japonica*; D, *Chelidonichthys spinosus*; E, *Peristedion orientale*; F, *Hoplichthys langsdorfii*. Scales indicate 5mm.

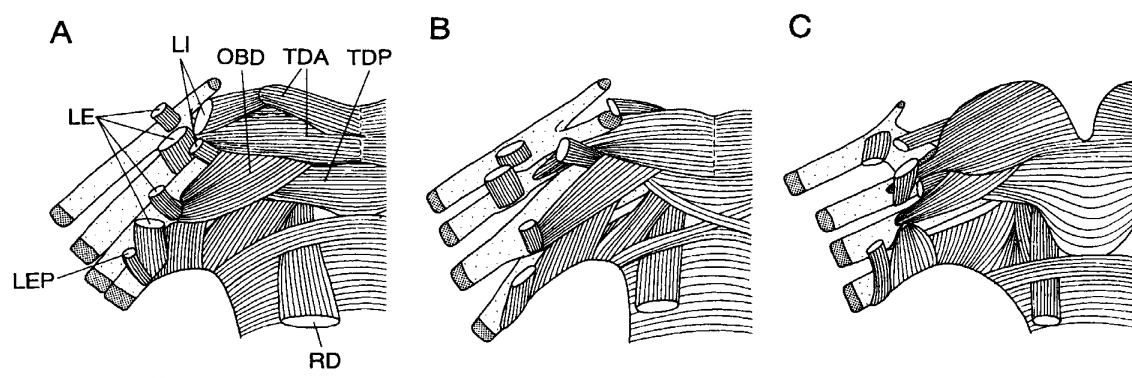


Fig. 6. Dorsal aspect of muscles serving upper branchial arches. A, *Parabembras curta*; B, *Bembradium roseum*; C, *Hoplichthys langsdorfii*. Scales indicate 5mm.

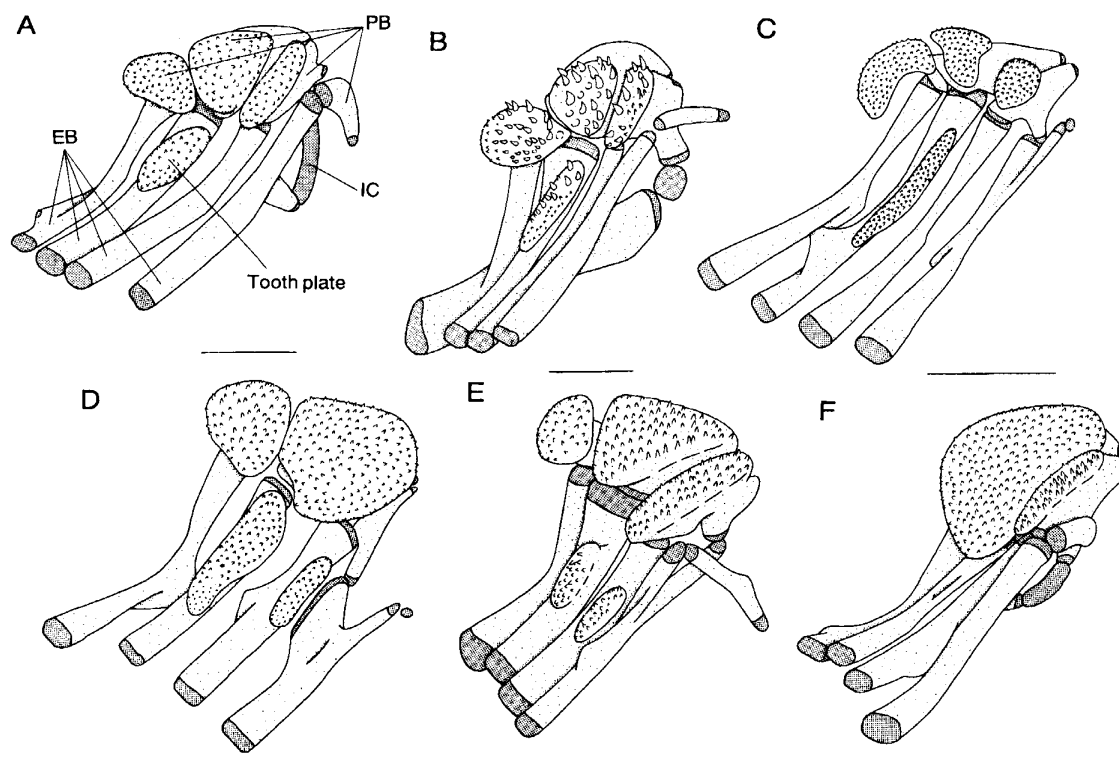


Fig. 7. Medial aspect of upper gill arch. A, *Parabembras curta*; B, *Bembras japonica*; C, *Bembradium roseum*; D, *Hoplichthys langsdorfii*; E, *Chelidonichthys spinosus*; F, *Peristedion orientale*. Scales indicate 5mm.

Clade B2. This clade is comprised of *Parabembras*, *Bembras*, Triglidae, Peristediidae, Hoplichthyidae and Platycephalidae. It is supported by one apomorphic character, actinosts being short and broad (31-1) (Fig. 8B). This clade branches into clades C1 and C2.

Clade C1. This clade includes only *Parabembras*, characterized by a derived character, the ascending process and remaining part of the premaxillary being separated (16-1).

Clade C2. This clade, which contains *Bembras*, Triglidae, Peristediidae, Hoplichthyidae and Platycephalidae, is supported by the following 3 characters: absence of the first spine on the first anal fin proximal pterygiophore (41-1) and presence of a soft second ray on the first anal fin proximal pterygiophore (42-1) and a soft ray on the second anal fin proximal pterygiophore (43-1). This clade is divided into the clades D1 and D2.

Clade D1. This clade, which includes only *Bembras*, has no defining apomorphic characters.

Clade D2. This clade, which includes Triglidae, Peristediidae, Hoplichthyidae and Platycephalidae, is supported by the following 4 characters: presence of a lateral opening on the pterotic continuous with the preopercle (9-1) (Fig. 20B), posteromedial parts of pelvic bones separated (36-1) (Figs 5E, F, 32), absence of the first spine on the first dorsal fin proximal pterygiophore (40-1) (Figs 33, 34B-D) and an unbranched transversus dorsalis anterior (55-1) (Figs 6C, 43A). Clade D2 is divided into subclades E1 and E2.

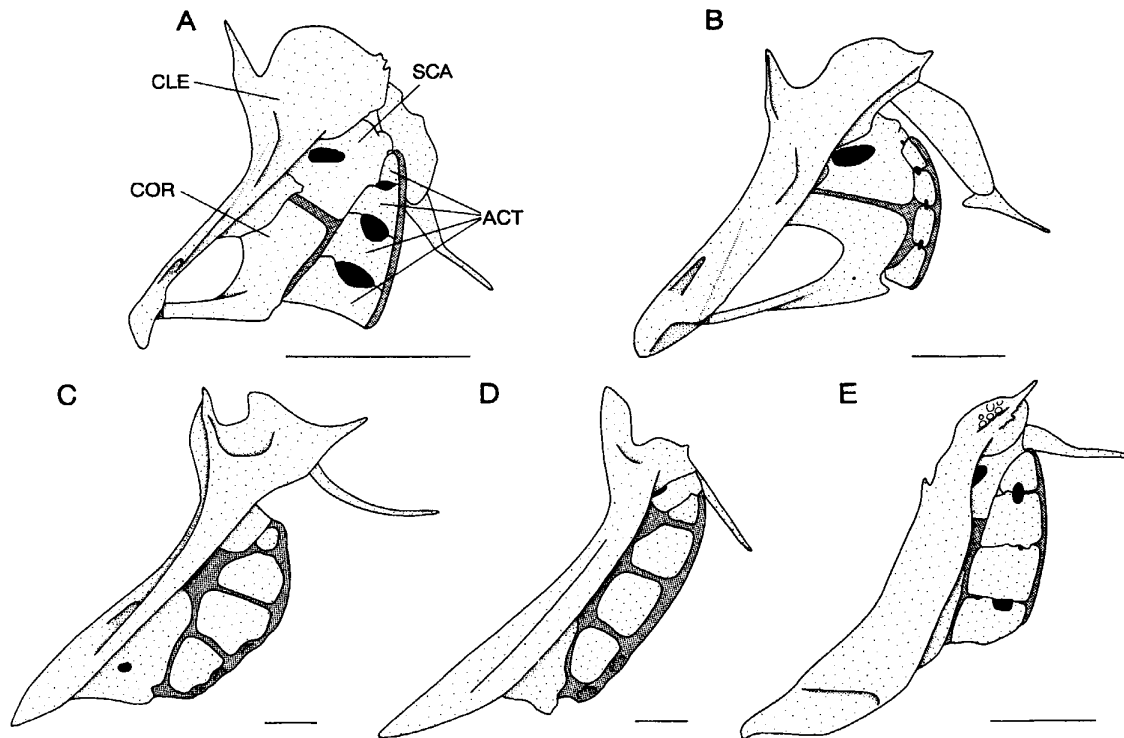


Fig. 8. Lateral aspect of pectoral girdle. A, *Plectrogenium nanum*; B, *Parabembras curta*; C, *Chelidonichthys spinosus*; D, *Satyrichthys serrulatus*; E, *Hoplichthys langsdorfii*. Scales indicate 5mm.

Clade E1. This clade includes Triglidae, Peristediidae and Hoplichthyidae, which share the following 15 characters: second infraorbital attached to the lateral ethmoid (5-1), tubercles present on the dorsal surface of the head (7-1) (Fig. 9), nasals sutured to the neurocranium (13-1), no notch between the ascending process and cranial condyle (17-1), a small entopterygoid (21-1), absence of an interarcual cartilage (26-1) (Fig. 7D, E), actinosts rectangular (31-2) (Fig. 8C-E), a broad cartilaginous band between the scapula and coracoid (32-1) (Fig. 8C-E), presence of lower free pectoral fin rays (33-1), fusion of the cartilaginous caps on the anterior portions of the pelvic bones (38-1) (Fig. 5D-F), urostyle fused with the upper hypural complex (50-1), transversus ventralis anterior and posterior separated (57-1), muscle bundles serving the free pectoral fin rays separated from the adjacent muscle (59-1), a division of bundles of the adductor superficialis serving the free pectoral fin rays (60-1) and dorsal elements of the pelvic muscles attached to the pectoral girdle (62-1). Clade E1 is divided into clades F1 and F2.

Clade F1. This clade, which includes Triglidae, is characterized by the attachment of the lachrymal and second infraorbital (3-1), attachment of the second and fourth infraorbitals (4-1), lateral ethmoids meeting in the middle (15-1) (Fig. 9B), articulation of the posteromedial portions of the pelvic bones (36-0[r]) (Fig. 5D), absence of the flexor ventralis externus (64-1) and presence of an intrinsic muscle (67-1).

In this clade, *Chelidonichthys*, *Lepidotrigla* and *Pterygotrigla* share the following characters: absence of teeth on the palatine (19-1) (Fig. 10C), absence of a basihyal

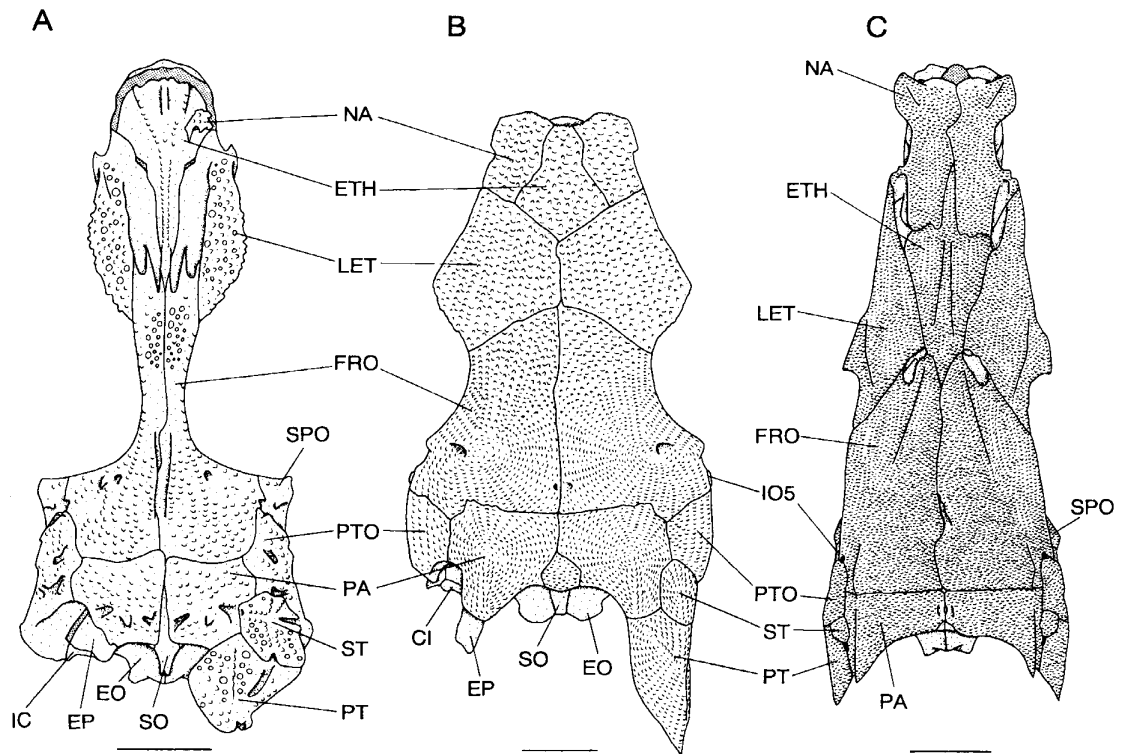


Fig. 9. Dorsal aspect of neurocranium. A, *Hoplichthys langsdorfii*; B, *Lepidotrigla microptera*; C, *Peristedion orientale*. Scales indicate 5mm.

(24-2), separation of the cartilaginous caps on the anterior portions of the pelvic bones (38-0[r]) and dorsal proximal pterygiophores being exposed along the first dorsal fin (49-1). *Chelidonichthys* and *Lepidotrigla* share: dorsal proximal pterygiophores being exposed along both dorsal fins (49-2), absence of an extrinsic muscle (66-0[r]) and there being more than two openings to the exterior in the lateral line scales (68-1). *Chelidonichthys* has the lateral ethmoids separated medially (15-0[r]) and fusion of the cartilaginous caps on the anterior portions of pelvic bones (38-1) (Fig. 5D), and *Lepidotrigla* has two tooth plates on the prevomer (8-1) and separation of the prootic and intercalar (11-1). *Pterygotrigla* is defined by the absence of tooth plates on the prevomer (8-2), Baudelot's ligament originating from the first vertebra (10-1), the obliquus superioris not extending to the neurocranium (65-1) and absence of an intrinsic muscle (67-0[r]). *Prionotus* and *Bellator* share the fifth infraorbital fused to the sphenotic (1-1), presence of the first spine on the first dorsal fin proximal pterygiophore (40-0[r]) and the urostyle being separated from the upper hypural complex (50-0[r]). *Prionotus* has two tooth plates on the prevomer (8-1), the lateral ethmoids separated medially (15-0[r]) and no extrinsic muscle (66-0[r]). *Bellator* has no apomorphic characters.

Clade F2. Clade F2 comprises Peristediidae and Hoplichthyidae. This clade is supported by Baudelot's ligament originating from the first vertebra (10-1), separation of the prootic and intercalar (11-1), slender dorsal spines (44-1), the parhypural fused with the first hypural (51-1), the hemal spine and third preural centrum being fused (52-1), obliquus superioris not extending to the neurocranium (65-1), all scales in the lateral line with a distinct spine (70-1) and the presence of bony plate-like lateral line scales (71-1). Clade F2 is divided into clades G1 and G2.

Clade G1. This clade includes Peristediidae. It is supported by the separation of the lachrymal and second infraorbital by the first infraorbital and ectopterygoid (3-2), absence of tooth plates on the prevomer (8-2), nasals on both sides sutured to each other (14-1) (Fig. 9C), absence of jaw teeth (18-1), absence of teeth on the palatines (19-1), a cartilaginous basihyal (24-1) (Fig. 11C), absence of a tooth plate on the third epibranchial (27-1) (Fig. 7F), third and fourth pharyngobranchials being fused (30-1) (Fig. 7F) and presence of bony plates on the body (73-1). In this clade, *Peristedion* has an interarcual cartilage (26-0 [r]) (Fig. 7F) and *Satyrichthys* has fusion of the second to fourth pharyngobranchials (30-2) and articulation of the

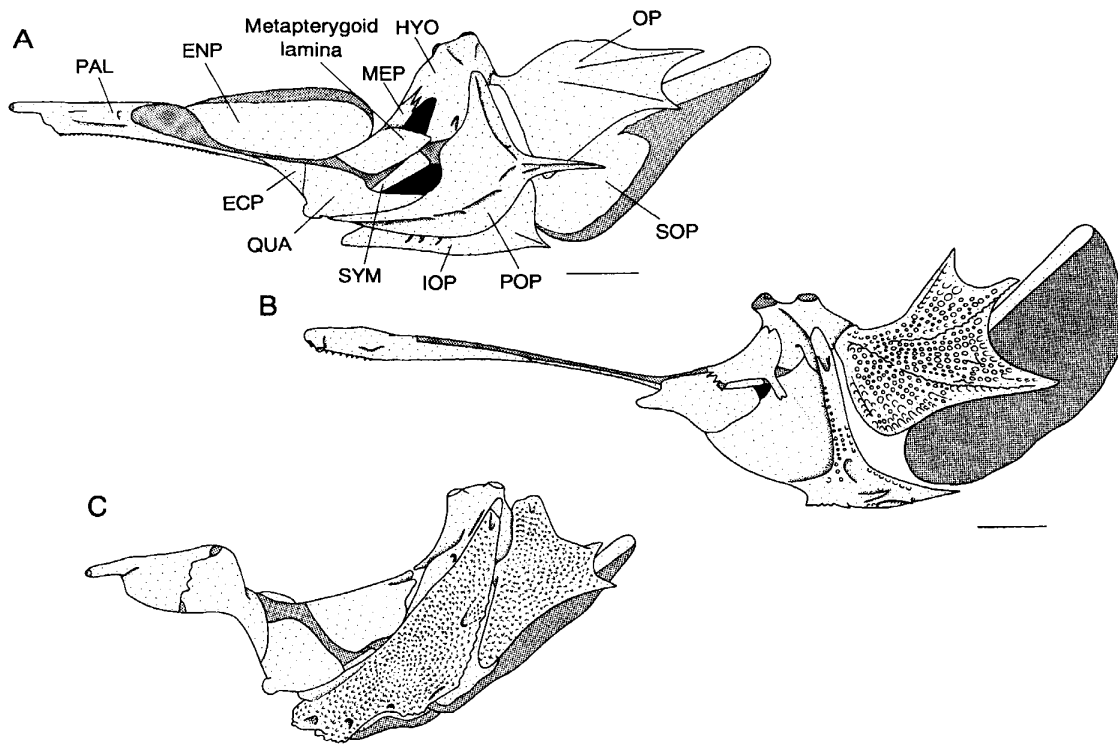


Fig. 10. Lateral aspect of suspensorium and opercular bones. A, *Parabembras curta*; B, *Hoplichthys haswelli*; C, *Lepidotrigla microptera*. Scales indicate 5mm.

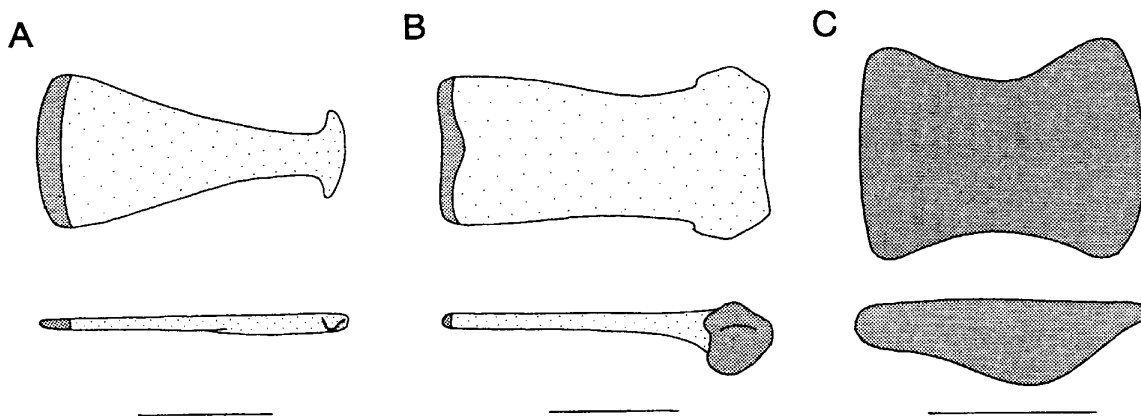


Fig. 11. Dorsal (upper) and lateral (lower) aspects of basihyal. A, *Parabembras curta*; B, *Hoplichthys langsdorfii*; C, *Satyrichthys serrulatus*. Scales indicate 3mm.

posteromedial portions of the pelvic bones (36-0 [r]).

Clade G2. This clade, containing Hoplichthyidae, is characterized by the following characters: fifth infraorbital fused to sphenotic (1-1) (Fig. 9A), second infraorbital and lateral ethmoid separated (5-0[r]), absence of a lateral opening on the pterotic continuous with the preopercle (9-0[r]) (Fig. 9A), absence of a sensory canal between the pterotic and preopercle (12-1), nasal and neurocranium loosely articulated (13-0[r]) (Fig. 9A), ascending process and remaining part of the premaxillary separated (16-1), a notch between the ascending process and cranial condyle (17-0[r]), absence of a metapterygoid lamina (20-1) (Fig. 10B), absence of the entopterygoid (21-2) (Fig. 10B), hypohyals and basihyal articulated (25-1) (facet for the articulation shown in Fig. 11B), a cartilaginous first pharyngo-branchial (28-1) (Fig. 7D), absence of a tooth plate on the second pharyngo-branchial (29-1) (Fig. 7D), absence of the levator posterior (56-1) (Fig. 6C), transversus ventralis anterior and posterior overlapping (57-0[r]), muscle bundles serving free pectoral fin rays not separated from the adjacent muscle (59-0[r]), no divisions of bundles of adductor superficialis serving free pectoral fin rays (60-0[r]) and absence of body scales, except on dorsal region (72-1). In this clade, *Hoplichthys langsdorfii* and *H. gilberti* share the protractor pectoralis comprising sheet-like anterior and robust posterior elements (58-1) and body scales entirely absent (72-2). *Hoplichthys gilberti* has the obliquus superioris extending to the neurocranium (65-0[r]) and *H. langsdorfii* has Baudelot's ligament absent (10-2) and all of the scales in the lateral line bearing two spines (70-2). *Hoplichthys haswelli* is characterized by the lack of attachment of dorsal elements of the pelvic fin muscles to the pectoral girdle (62-0[r]).

Clade E2. This clade, containing Platycephalidae, is defined by the following six apomorphic characters: ascending process and remaining part of the premaxillary separated (16-1) (Fig. 21), urohyal and first basibranchial sutured (23-1) (Fig. 27), absence of a second element on the first anal fin proximal pterygiophore (42-2) (Fig. 33B), sternohyoideus inserted onto both the lateral and ventral aspects of the urohyal (54-1) (Fig. 42B), protractor pectoralis comprising sheet-like anterior and robust posterior elements (58-1) (Fig. 45) and adductor superficialis pelvici connected to pelvic fin rays via a long strong tendon (61-1) (Fig. 46).

Definition of ingroup and outgroups for second step. The phylogenetic relationships of the Platycephaloidei, except those among Platycephalidae, were determined in the first-step analysis. Platycephalidae is here defined as the ingroup. The polarity of ingroup characters was determined by using *Plectrogenium*, *Bembradium*, *Parabembras*, *Bembras* and the platycephalid sister group, including Triglidae, Peristediidae and Hoplichthyidae, as outgroups, for the second-step analysis. Other scorpaenoids were not used, because the relationships of the scorpaenoids became unclear after the first-step analysis.

Comparative anatomy of Platycephalidae

In this section, the osteological and myological characters of platycephalids are described and figured under the rubric "Description." Characters that varied among platycephalids are listed under "Characters." Characters in the outgroups and outgroup node (ON) are mentioned under "Outgroups" and "Polarity," respectively.

The treatment of characters ("ordered" or "unordered") in multistate transformation series is noted in parentheses after "Polarity," where relevant.

I. Osteology

Circumorbital bones (Fig. 12)

Description

The circumorbital bones comprise one lachrymal and five infraorbitals, forming a serial tubular structure for the infraorbital sensory canal. The suborbital ridge is usually spiny, although *Platycephalus*, *Neoplatycephalus* and *Thysanophrys cirronasa* lack prominent spines (Fig. 12A). The suborbital ridge is finely serrated in *Onigocia*, *Suggrundus jugosus*, *Rogadius*, *Sorsogona* and *Grammoplites portuguesus* (Fig. 12G, H).

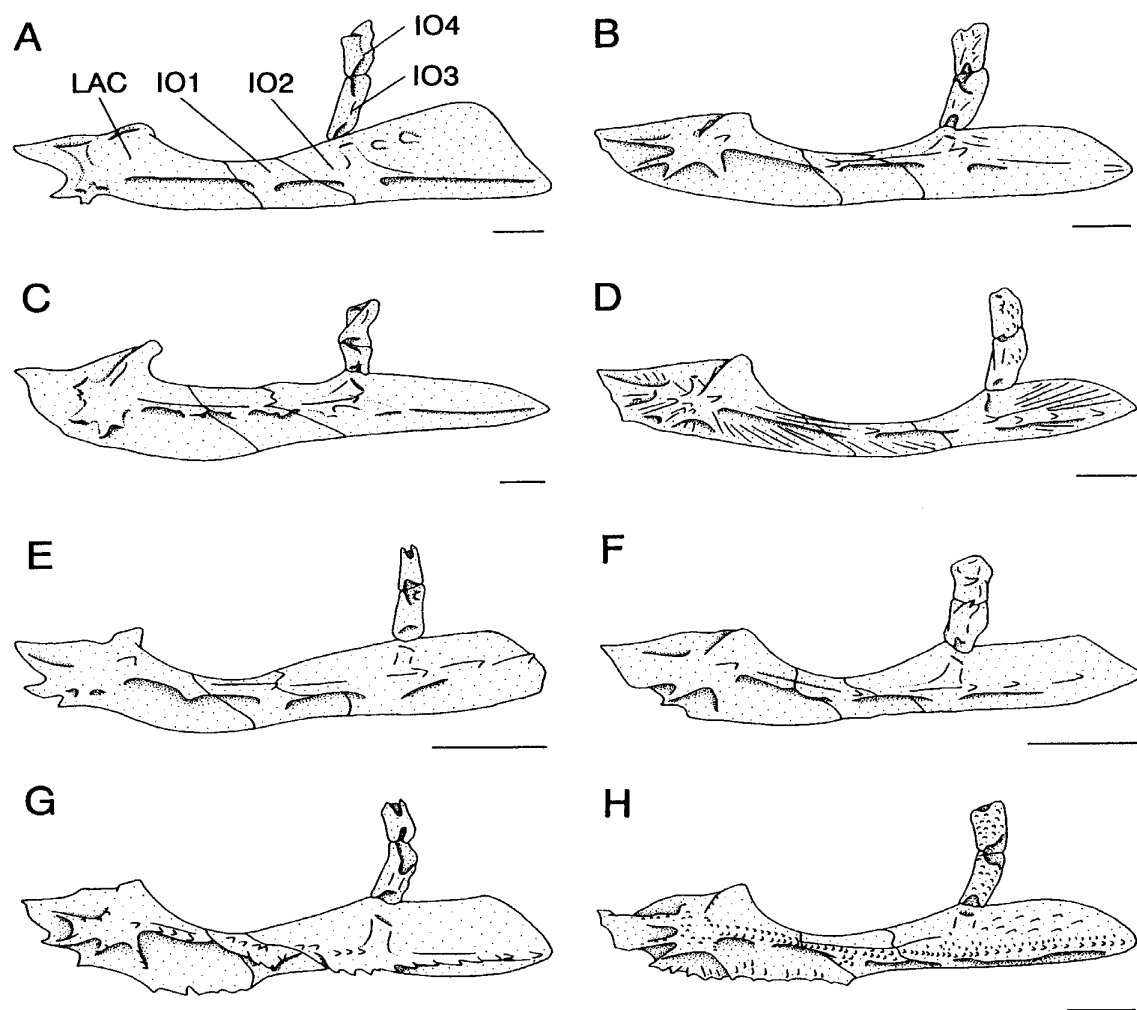


Fig. 12. Lateral aspect of circumorbital bones. A, *Neoplatycephalus richardsoni*; B, *Cociella crocodila*; C, *Cymbacephalus nematophthalmus*; D, *Suggrundus rodericensis*; E, *Thysanophrys armata*; F, *Grammoplites gruveli*; G, *Onigocia macrolepis*; H, *Rogadius asper*. Scales indicate 5mm.

The triangular lachrymal, situated in front of the circumorbital bones, is sutured to the first infraorbital posteriorly and articulates with the lateral ethmoid dorsally.

The first infraorbital is a rectangular bone, sutured to the lachrymal anteriorly and second infraorbital posteriorly.

The second infraorbital, an elongate plate-like bone, is firmly attached to the first infraorbital anteriorly. Its broad posterior border extends backward and is connected with the preopercle. The tubular structure has an upward opening for the sensory canal that runs, which is continuous with the supraorbital sensory canal that runs through the third to fifth infraorbital bones. A suborbital shelf is absent.

The remaining infraorbitals are small, rectangular bones, the third and fourth being situated between the neurocranium and second infraorbital. The fifth infraorbital is firmly attached to the dorsal surface of the sphenotic (figured with the neurocranium in Figs 13-17).

Characters

TS 74. Serrated suborbital ridge

0: absent; 1: present. The serrated condition is found only in *Onigocia*, *Suggrundus jugosus*, *Rogadius*, *Sorsogona* and *Grammoplites portuguesus*.

Outgroups. The condition is absent in all outgroups, except *Bembradium*, which has a finely serrated ridge.

Polarity. ON = 0.

TS 75. Spines on suborbital ridge

0: prominent spine(s) present; 1: prominent spines absent. No prominent spines of the ridge are present in *Platycephalus*, *Neoplatycephalus* and *Thysanophrys cirronasa*.

Outgroups. The suborbital ridge has several prominent spines in all outgroups, except all triglids and the peristediid, *Peristedion*.

Polarity. ON = 0.

Other variations

Preorbital spine. The preorbital spine is usually present in platycephalids, except in *Platycephalus*, *Neoplatycephalus*, *Inegocia*, *Papilloculiceps* and *Cymbacephalus*. However, intraspecific variation (presence and absence) is found in, at least, *Thysanophrys chiltonae*. Accordingly, presence or absence of the spine was not used in the analysis.

Neurocranium (Figs 13-20)

Description

The neurocranium is comprised of six unpaired elements (prevomer, ethmoid, parasphenoid, basisphenoid, supraoccipital and basioccipital) and eleven paired elements (nasal, lateral ethmoid, frontal, pterosphenoid, sphenotic, prootic, parietal, pterotic, epiotic, intercalar and exoccipital). The dorsal surface of the neurocranium is usually spiny, with many tubercles also being present in *Sorsogona*, *Rogadius*, *Grammoplites suppositus*, *G. portuguesus* and *Suggrundus*, except *S. jugosus* (Fig. 16).

The nasal is a flat bone, connected with the anterior process of the ethmoid posteromedially. It occupies the anterior part of the supraorbital sensory canal that comes from the frontal and often has a backwardly-directed spine dorsally.

The prevomer is a triangular bone, situated anteroventrally on the neurocranium. It has two separated tooth plates ventrally in all platycephalids (Figs

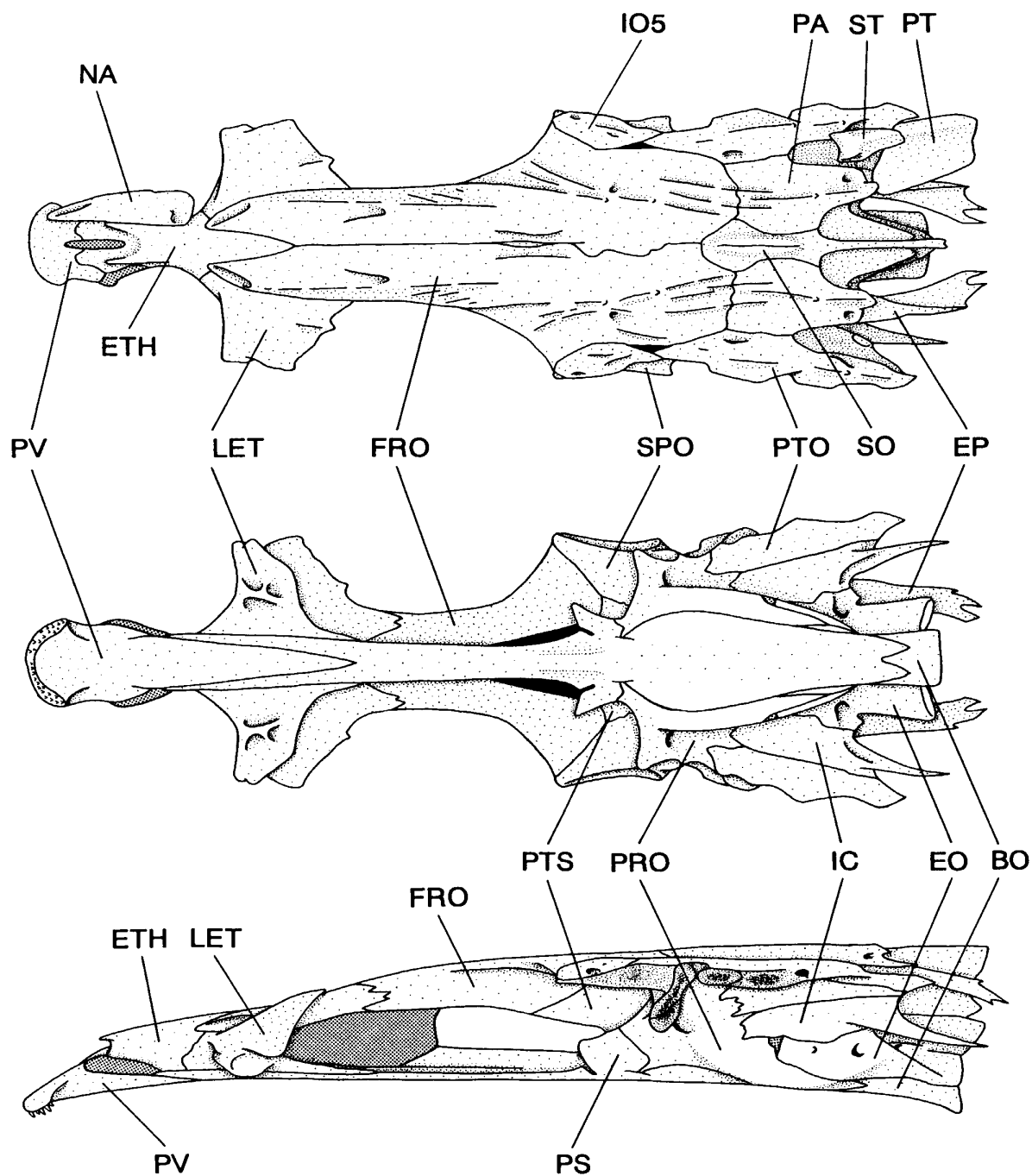


Fig. 13. Neurocranium of *Neoplatycephalus conatus* in dorsal (upper), ventral (middle) and lateral (lower) aspects. Scale indicates 10mm.

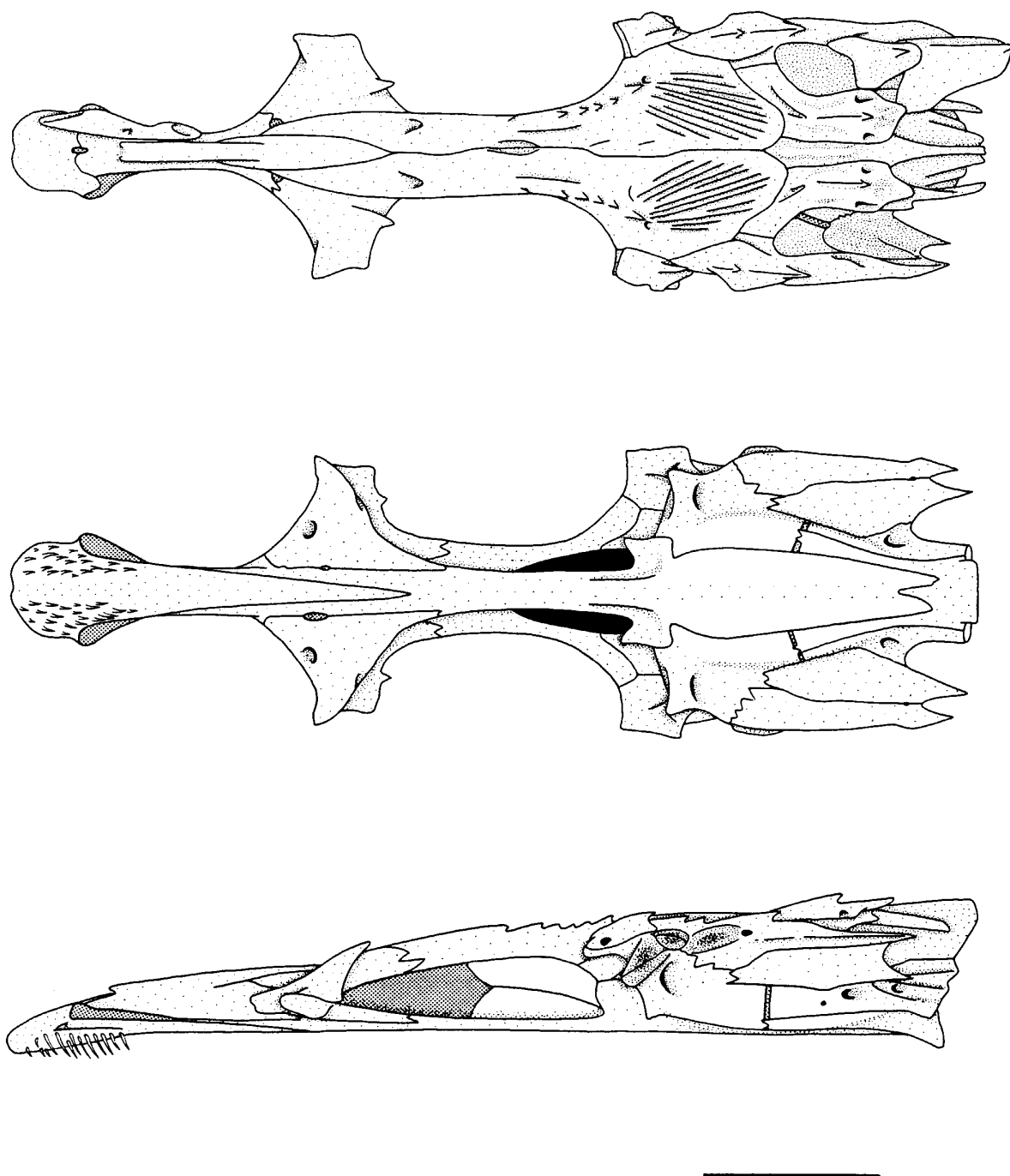


Fig. 14. Neurocranium of *Ratabulus megacephalus* in dorsal (upper), ventral (middle) and lateral (lower) aspects. Scale indicates 10mm.

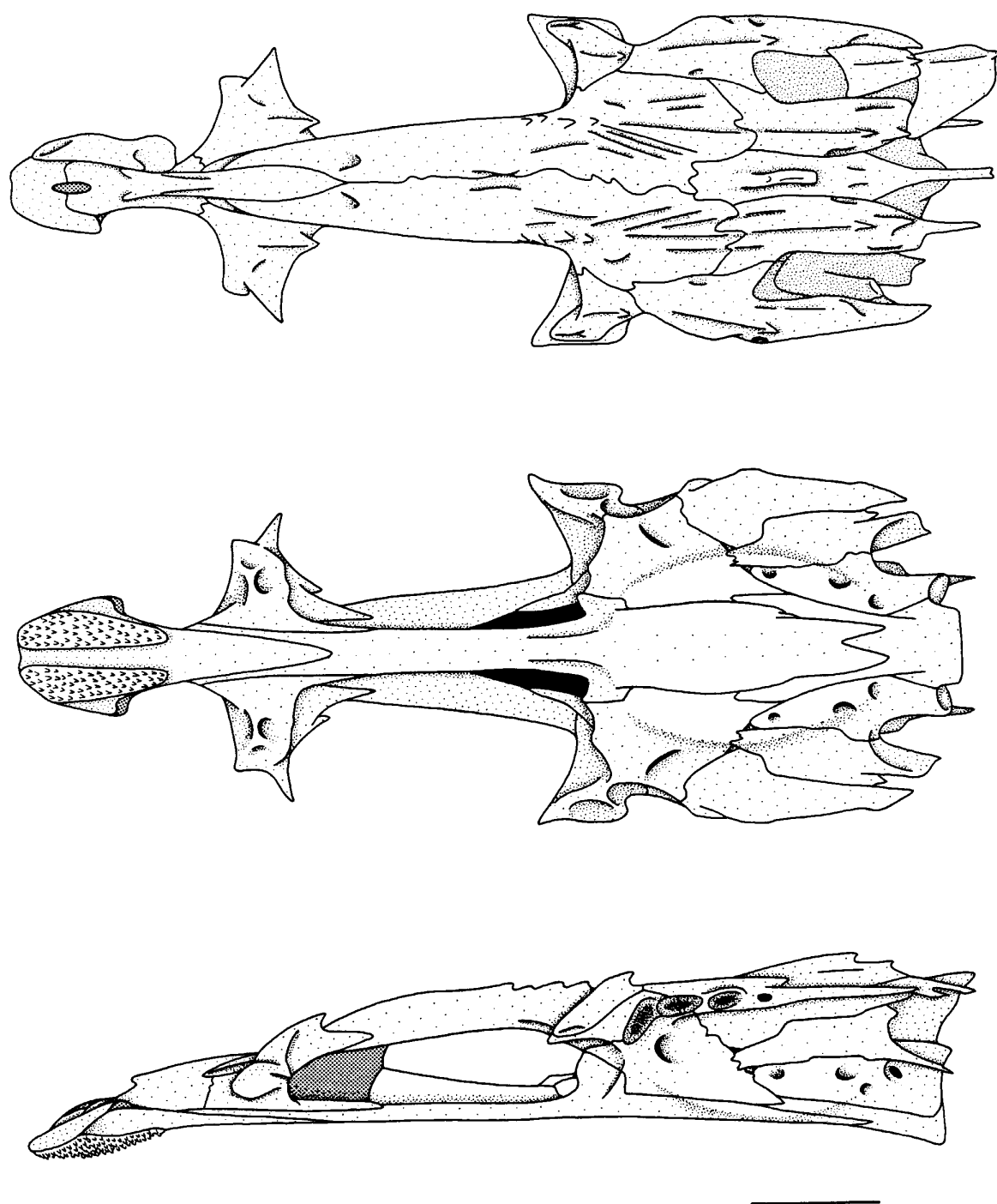


Fig. 15. Neurocranium of *Cymbacephalus nematophthalmus* in dorsal (upper), ventral (middle) and lateral (lower) aspects. Scale indicates 10mm.

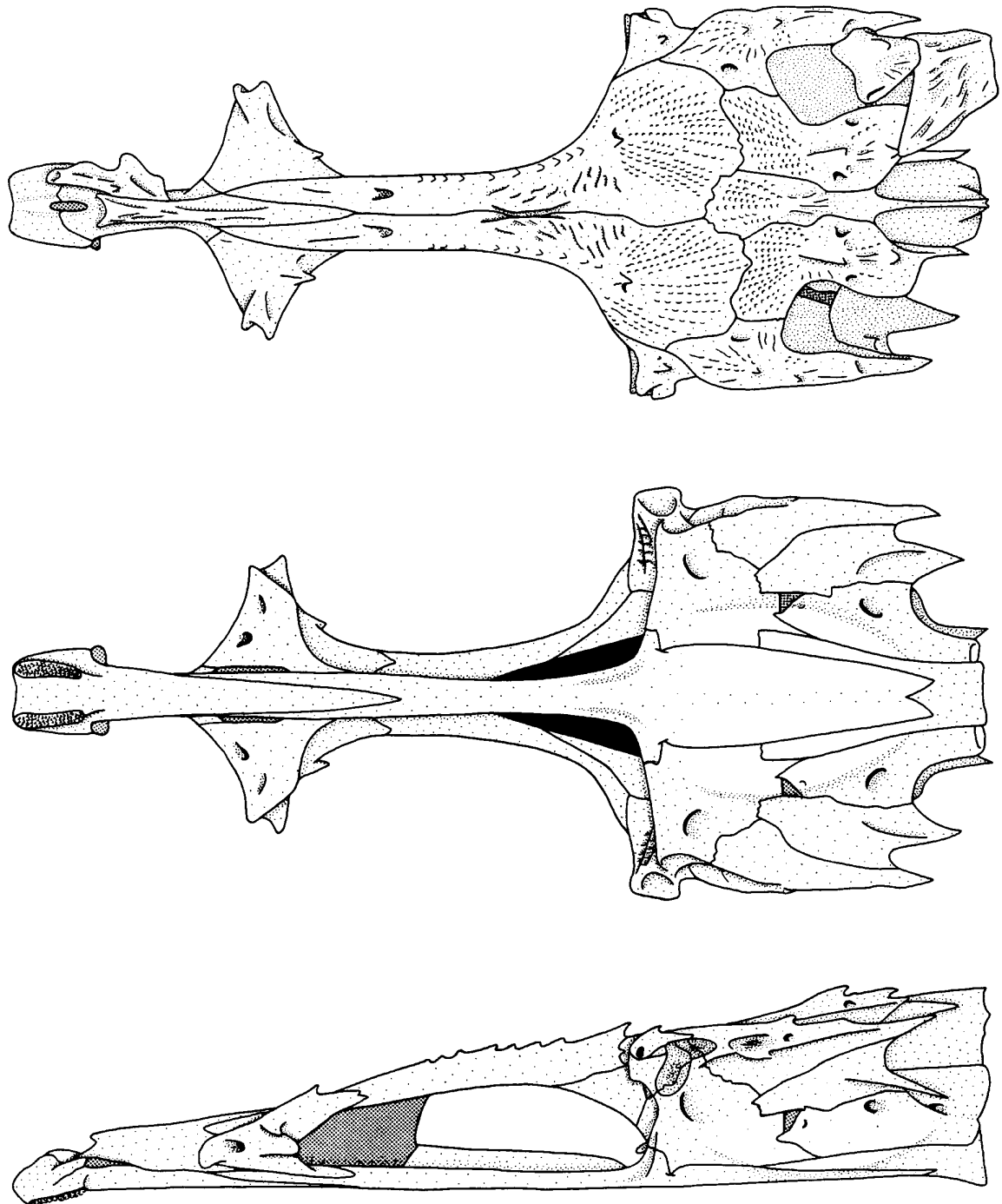


Fig. 16. Neurocranium of *Suggrundus rodericensis* in dorsal (upper), ventral (middle) and lateral (lower) aspects. Scale indicates 10mm.

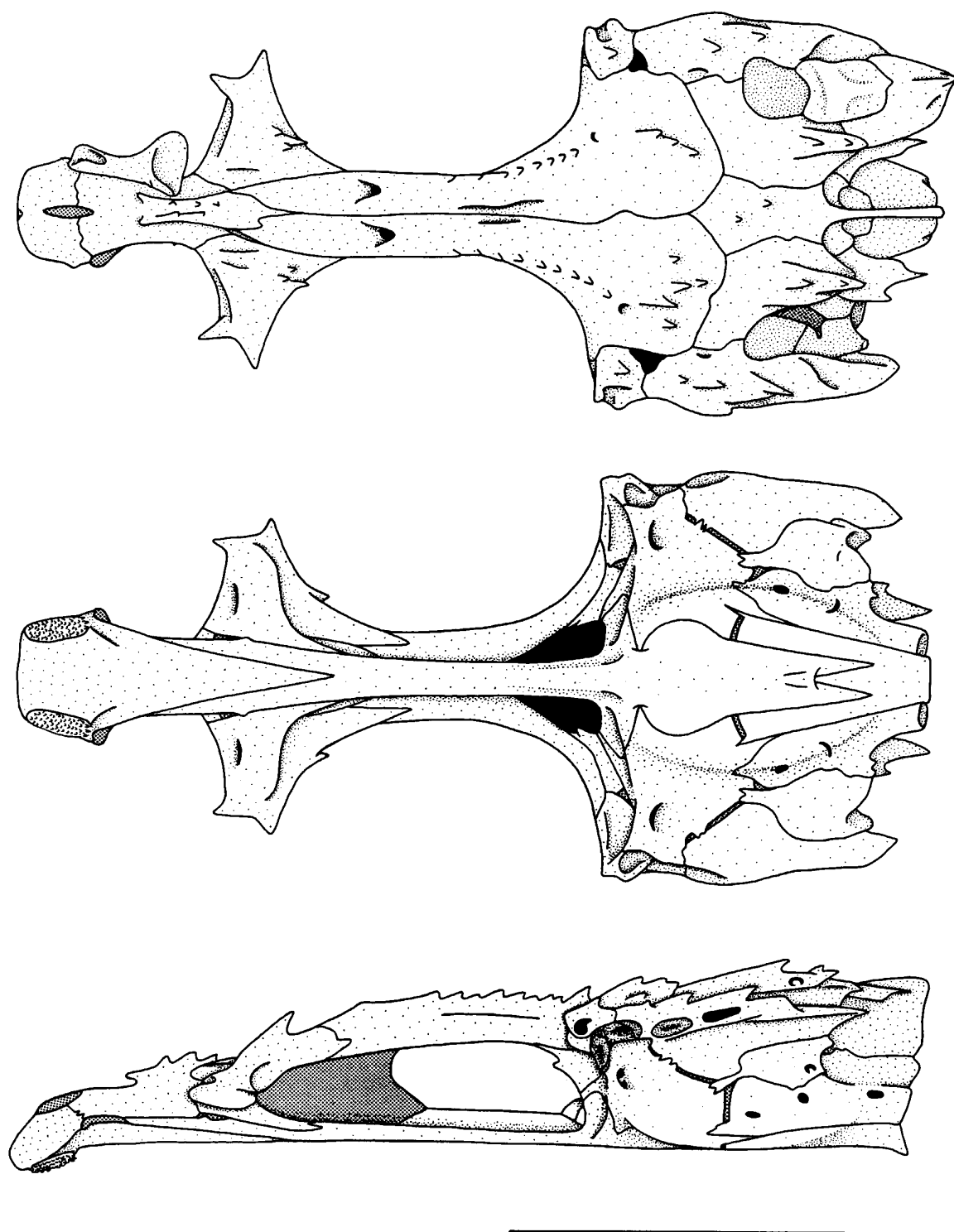


Fig. 17. Neurocranium of *Onigocia macrolepis* in dorsal (upper), ventral (middle) and lateral (lower) aspects. Scale indicates 10mm.

14-17), except *Platycephalus* and *Neoplatycephalus*, which have a single continuous tooth plate (Fig. 13). It is connected with the ethmoid dorsally, the lateral ethmoid laterally and the parasphenoid ventrally. It is also connected anterolaterally with the palatine by a strong ligament. A narrow strip of cartilage covers this bone posteromedially.

The ethmoid forms the anterior border of the neurocranium and is connected with the prevomer anteriorly, the lateral ethmoid laterally and the frontals posteriorly. The ethmo-premaxillary ligament (*sensu* Stiasny 1986) connects the anterior process of this bone with the lateral process of the maxillary.

The lateral ethmoid is connected with the frontal dorsally, the ethmoid anteriorly and the parasphenoid ventrally, and articulates with the dorsal process of the lachrymal laterally. A strong preocular spine is present in all platycephalids (Figs 13-16), except *Grammoplites portuguesus*, *Sorsogona* and *Onigocia spinosa*, which have several spines around the anterior orbit (Fig. 18).

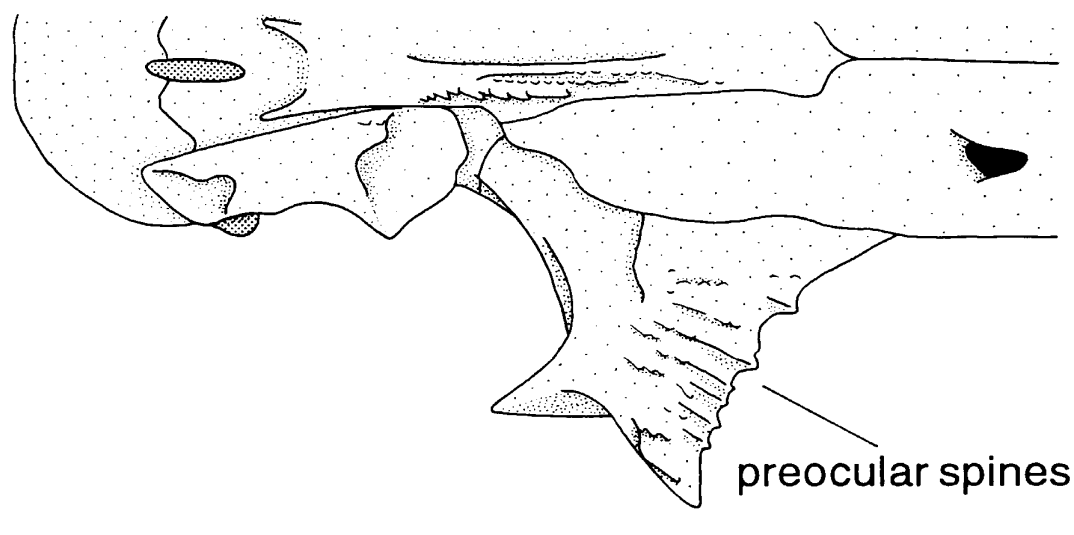


Fig. 18. Dorsal aspect of anterior part of neurocranium in *Sorsogona nigripinna*. Scale indicates 3mm.

The frontal is the largest bone of the dorsal skull roof, contacting the ethmoid anteriorly, the lateral ethmoid anterolaterally, the pterosphenoid ventrally, the sphenotic, fifth infraorbital and pterotic posterolaterally, and the parietal and supraoccipital posteriorly. It includes the supraorbital sensory canal, which is continuous with the canals of the nasal anteriorly and fifth infraorbital laterally.

The parietal forms the posterodorsal roof of the neurocranium, meeting the epiotic posteriorly, the supraoccipital medially, the frontal anteriorly and the pterotic laterally. It bears a backwardly-directed spine, below which runs the supratemporal sensory canal.

The sphenotic forms the posterodorsal corner of the orbit, usually being sutured to the frontal anteromedially, the pterotic posteriorly, the pterosphenoid anteroventrally, the prootic ventrally and the fifth infraorbital dorsally. It has a lateral socket for the anterodorsal condyle of the hyomandibular.

The pterosphenoid forms the posterodorsal wall of the orbit and is connected

with the frontal anteriorly, the prootic (and the parasphenoid) ventrally, and the sphenotic laterally. It is also connected ventrally with the basisphenoid in *Platycephalus*, *Neoplatycephalus*, *Elates* and *Thysanophrys*, except *T. arenicola* and *T. otaitensis*. The pterosphenoid has a lateral foramen in *Platycephalus*, except *P. longispinis* (Fig. 19).

The parasphenoid is a long bone, situated on the mid-ventral wall of the neurocranium. It is usually connected with the prevomer, lateral ethmoid and ethmoid anteriorly, the basisphenoid medially, the prootic laterally and the basioccipital posteriorly. The wing-like process on the parasphenoid is simple in all platycephalids, except *Neoplatycephalus conatus*, *Platycephalus caeruleopunctatus*, *P. marmoratus* and *P. fuscus*, where it is bilobed in shape (Fig. 19).

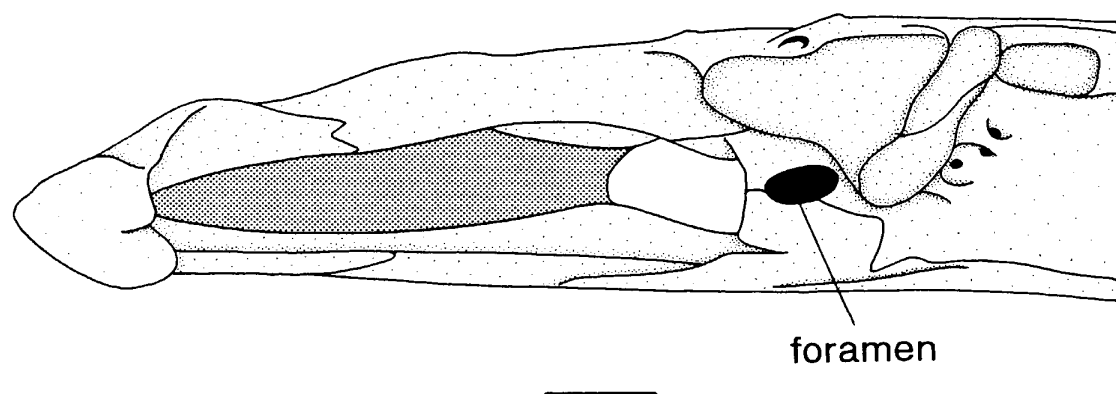


Fig. 19. Lateral aspect of middle part of neurocranium in *Platycephalus caeruleopunctatus*. Scale indicates 5mm.

The basisphenoid bridges the posteroventral margin of the orbit, usually being sutured to the prootic posteriorly and the parasphenoid anteroventrally. It is also sutured posterodorsally to the pterosphenoid in *Platycephalus*, *Neoplatycephalus*, *Elates* and *Thysanophrys*, except *T. arenicola* and *T. otaitensis*.

The prootic forms the auditory bulla. It is connected with the pterosphenoid anteriorly, the basisphenoid anteromedially, the basioccipital, exoccipital and intercalar posteriorly, the sphenotic and pterotic dorsally, and the parasphenoid ventrally.

The pterotic forms the dorsolateral part of the neurocranium, in addition to forming the posttemporal fossa with the parietal and epiotic. It is connected with the frontal and the sphenotic anteriorly, and the parietal and epiotic medially. This bone receives sensory canals from the fifth infraorbital anteriorly, the supratemporal medially and the preopercle posterolaterally. A lateral opening, continuous with the preoperculo-mandibular sensory canal, occurs in all platycephalids (Fig. 20B).

The epiotic is situated on the posterior region of the neurocranium and is sutured to the parietal dorsally, the supraoccipital medially, the pterotic ventrally and the exoccipital posteriorly. It has a long projection posteriorly.

The intercalar forms the posteroventral wall of the neurocranium, being connected with the prootic anteriorly, the pterotic laterally and the exoccipital medially. The posteromedial region of the intercalar forms a facet for its connection with the ventral limb of the posttemporal.

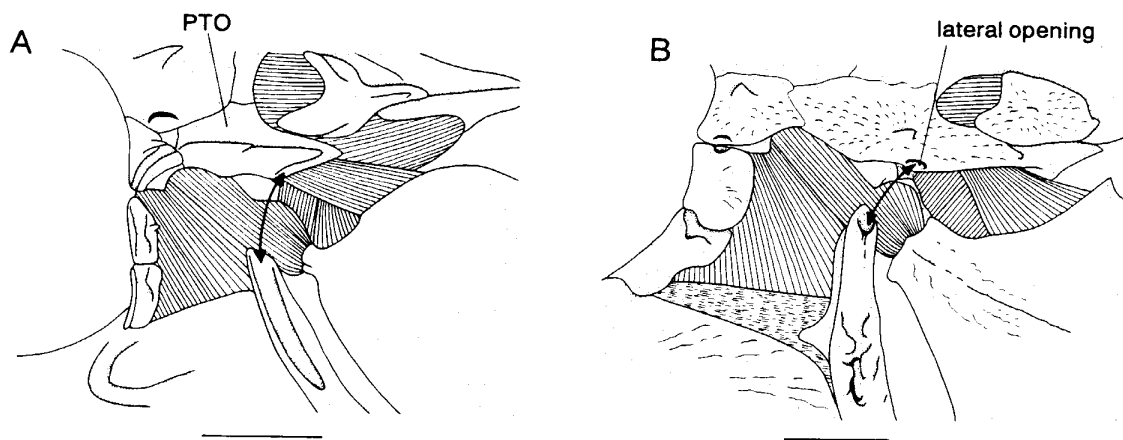


Fig. 20. Dorsolateral aspects of posterior part of neurocranium. A, *Parabembras curta* (outgroup); B, *Suggrundus cooperi*. Scale indicates 5mm.

The supraoccipital forms the posteromedial roof of the neurocranium, meeting the frontal anteriorly, the parietal and epiotic laterally, and the exoccipital ventrally. A supraoccipital crest is well developed.

The exoccipital forms the posteromedial wall of the neurocranium, contacting the supraoccipital dorsally, the prootic anteriorly, the intercalar and pterotic dorsolaterally, and the basioccipital ventrally. It has a posterior condyle for articulation with the first vertebra.

The basioccipital forms the posteroventral position of the neurocranium, meeting the exoccipital dorsally, the prootic anteriorly and the parasphenoid ventrally. It has a posterior condyle for articulation with the first vertebra. Baudelot's ligament originates from the lateral surface of this bone.

Characters

TS 76. Tubercles on head

0: absent; 1: present. Tubercles are present in *Sorsogona*, *Rogadius*, *Grammoplites suppositus*, *G. portuguesus* and *Suggrundus*, except *S. jugosus*.

Outgroups. Tubercles are found in all triglids, peristediids and hoplichthyids (Fig. 9), but are absent in the others.

Polarity. ON=0 or 1.

TS 77. Number of preocular spines around orbit

0: none; 1: one spine; 2: several spines. *Sorsogona*, *Onigocia spinosa* and *Grammoplites portuguesus* have more than two preocular spines.

Outgroups. Whereas *Chelidonichthys* and *Satyrichthys* have several preocular spines, prominent spines are lacking in *Lepidotrigla*, *Pterygotrigla*, *Prionotus* and all hoplichthyids. Other outgroups have one spine (Fig. 9).

Polarity. ON=0 or 1 (ordered as 0-1-2).

TS 78. Number of tooth plates on prevomer

0: one; 1: two. Two plates with teeth are present in all platycephalids, except *Platycephalus* and *Neoplatycephalus*.

Outgroups. *Bembradium*, *Lepidotrigla* and *Prionotus* have two separated tooth plates, whereas *Pterygotrigla* and all peristediids lack tooth plates. Other outgroups have one plate.

Polarity. ON=0.

TS 79. Foramen on pterosphenoid

0: absent; 1: present. A foramen is found on the pterosphenoid in *Platycephalus*, except *P. longispinis*.

Outgroups. A foramen is absent in all outgroups.

Polarity. ON=0.

TS 80. Basisphenoid

0: contacting prootic; 1: contacting prootic and pterosphenoid; 2: absent. This bone contacts with the prootic and pterosphenoid posteriorly in *Platycephalus*, *Neoplatycephalus*, *Elates*, *Thysanophrys cirronasa*, *T. chiltonae* and *T. armata*.

Outgroups. *Bembras* has the basisphenoid in contact with the prootic and pterosphenoid. A basisphenoid is absent in *Prionotus*, *Bellator*, peristediids and hoplichthyids, but is present, contacting the prootic posteriorly, in the remaining outgroups.

Polarity. ON=0, 1 or 2 (unordered).

Remarks. This variation in the basisphenoid was not used in the first-step analysis, because percoids have both conditions equally (basisphenoid in contact with the prootic or with the prootic and pterosphenoid) and the polarity is unclear.

TS 81. Wing-like process of parasphenoid

0: simple; 1: bilobed. A bilobed process is present in *Neoplatycephalus conatus*, *Platycephalus caeruleopunctatus*, *P. marmoratus* and *P. fuscus*.

Outgroups. All outgroups have a simple process.

Polarity. ON=0.

Other variations

Spines around a strong preocular spine. In *Onigocia macrolepis* (HUMZ 49467) and *Suggrundus jugosus* (AMS I.20845-001), a few small spines are present around a strong preocular spine (Fig. 17). This feature is apomorphic, because no outgroups have such a condition. It was not used for the analysis, since some specimens of the above species lack the spines, suggesting intraspecific variation.

Parietal and epiotic. Fusion of the parietal and epiotic is found in *Suggrundus macracanthus*, *S. rodericensis*, *Cymbacephalus nematophthalmus*, *Sorsogona tuberculata* and *Grammoplites scaber*, the bones being separated in other species. Although fusion may be apomorphic, owing to its non-occurrence in the outgroups, intraspecific variation was observed in *Suggrundus meerdervoortii*. Moreover, the bones are fused only partially in a specimen of *Inegocia japonica* (HUMZ 5204).

Parasphenoid and pterosphenoid. The parasphenoid is attached to the pterosphenoid at least in *Cymbacephalus*, *Elates*, *Grammoplites scaber*, *G. suppositus*, *Inegocia*, *Neoplatycephalus*, *Papilloculiceps*, *Platycephalus*, except *P. longispinis*, *Ratabulus*, *Rogadius pristiger*, *Suggrundus jugosus* and *Thysanophrys cirronasa*. On the other hand, the two bones are separated by the prootic in other groups. However, this variation was not used in the analysis, since the parasphenoid contacts the pterosphenoid on the left side only in a specimen of *Cociella crocodila* (HUMZ 35250).

Basisphenoid and parasphenoid. The basisphenoid is usually attached to the parasphenoid anteriorly in the platycephalids, but it is separated from the latter in *Thysanophrys arenicola*, *T. otaitensis*, *Rogadius asper*, *R. pristiger*, *Grammoplites gruveli* and *Sorsogona tuberculata*. However, this variation could not be used, because intraspecific variation occurs in *Suggrundus rodericensis*.

Jaws (Figs 21, 22)**Description**

The jaws include the premaxillary and maxillary in the upper jaw, and the dentary, anguloarticular, retroarticular and coronomeckelian in the lower jaw. Cartilaginous elements, the rostral cartilage (upper jaw) and Meckelian cartilages (lower jaw), are also present. A supramaxillary is absent.

The premaxillary has four processes: ascending process, articular process, alveolar process and postmaxillary process. The ascending process, having a rostral cartilage posteriorly, is separated from the remaining part of the premaxillary in all

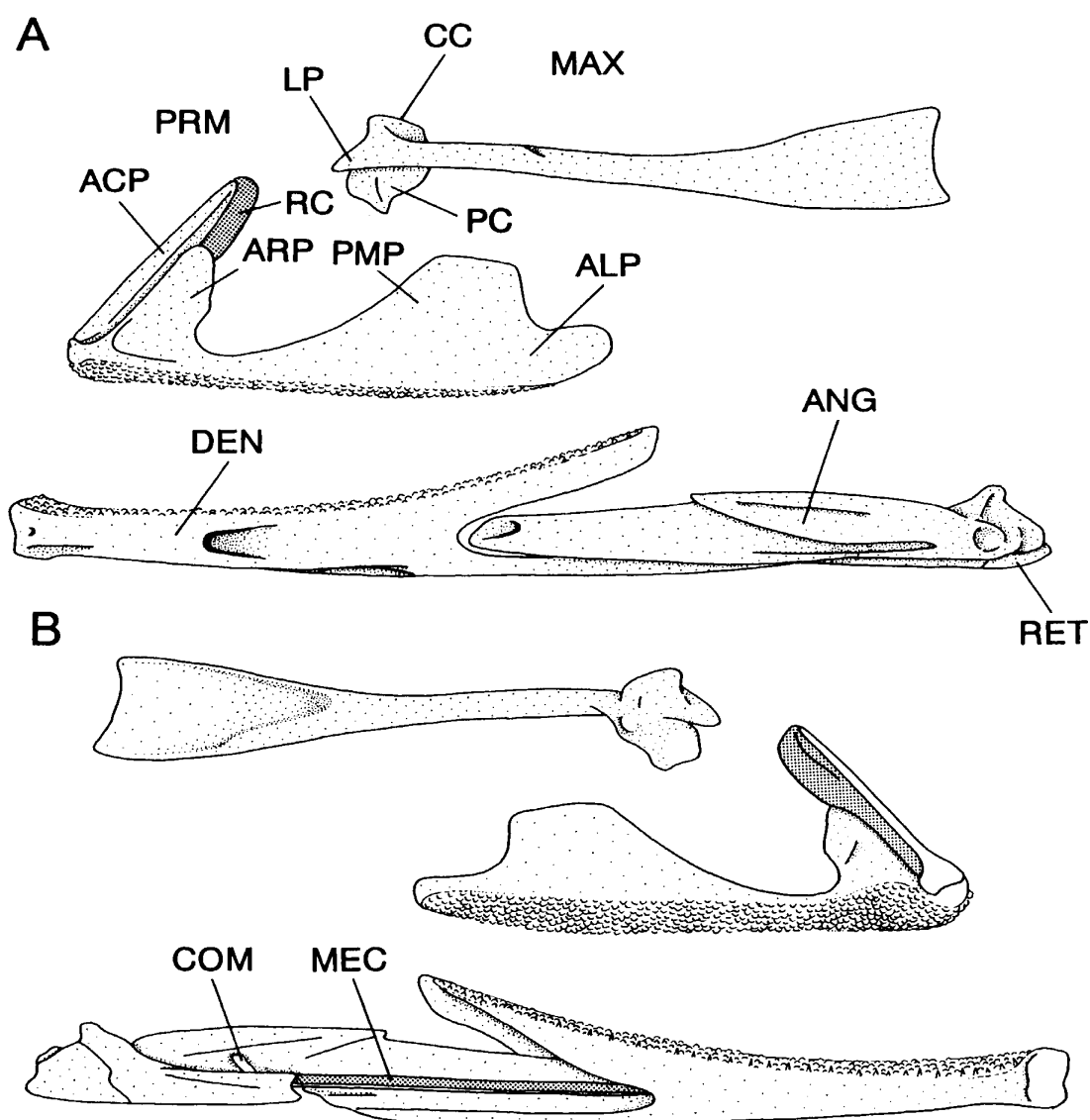


Fig. 21. Lateral (A) and medial (B) aspects of maxillary (upper), premaxillary (middle) and lower jaw (lower) in *Inegocia japonica*. Scale indicates 5mm.

platycephalids (Fig. 21). A deep notch is present between the ascending process and articular process. The alveolar process has a tooth plate on its ventral aspect, usually with villiform or small, canine-like teeth, although long, slender canine teeth are present in *Ratabulus* (Fig. 22A).

The maxillary consists of a head, bearing a lateral process, premaxillary condyle and cranial condyle, and a long shaft. The lateral process and premaxillary condyle sandwich the articular process of the premaxillary. A slender ligament connects the lateral process with the anterior process of the ethmoid. The cranial condyle articulates with the anterolateral surface of the rostral region of the neurocranium. The basal portion of the cranial condyle articulates with the anterior process of the palatine. The ligamentum primordium is inserted onto the anterolateral surface of the shaft, and a tendon from the adductor mandibulae section A1 is inserted onto the posterior surface of the premaxillary condyle.

The dentary is a toothed bone, and has a tubular structure forming the anterior

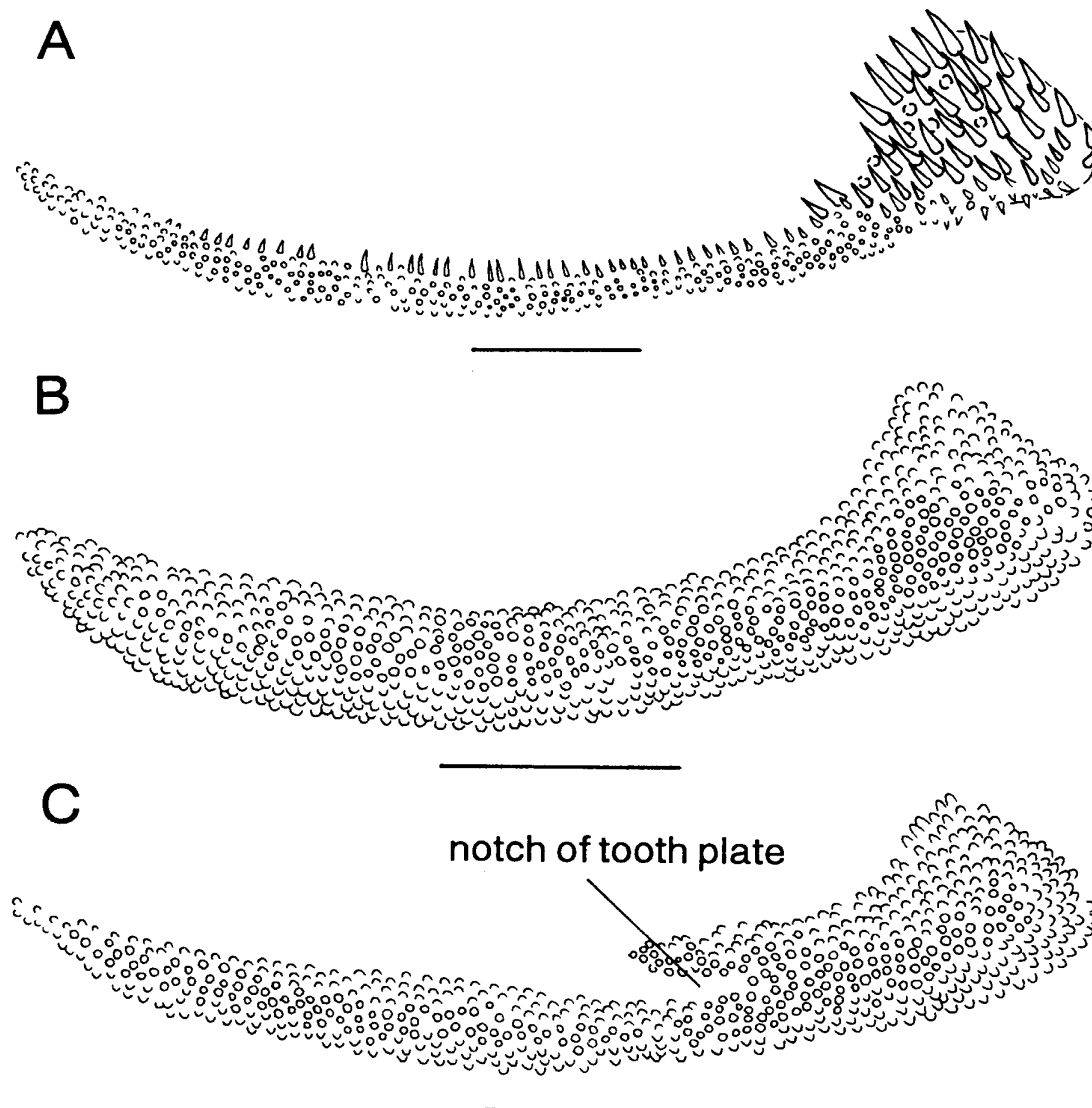


Fig. 22. Dentition of upper jaw (ventral aspect of left premaxillary). A, *Ratabulus megacephalus*; B, *Grammoplites scaber*; C, *Cociella crocodila*. Scales indicate 3mm.

portion of the preoperculo-mandibular sensory canal ventrally. It is connected with the anguloarticular posteriorly and the Meckelian cartilage medially.

The anguloarticular forms the posterior portion of the lower jaw, its anterior projection being inserted into the deep notch of the dentary. It articulates dorsolaterally with the condyle of the quadrate and is attached to the retroarticular ventrally. The Meckelian cartilage lies on its medial surface. A coronomeckelian is situated in the gap between the anguloarticular and the Meckelian cartilage.

The retroarticular forms the posteroventral corner of the lower jaw, being attached to the anguloarticular anterodorsally and having a strong ligamentous connection with the interopercle.

The coronomeckelian is a tiny bone, situated on the medial surface of the anguloarticular near the posterior end of the adductor mandibulae. This bone is absent in *Elates*.

Characters

TS 82. Teeth on jaws

0: villiform or small canine teeth; 1: long, slender canine teeth. All platycephalids, except *Ratabulus*, which has long, slender canine teeth, possess villiform or small canine jaw teeth.

Outgroups. All outgroups, except peristediids, in which teeth are absent, have villiform or small canine jaw teeth.

Polarity. ON = 0.

Remarks. *Ratabulus* has long canine teeth, not only on the jaws, but also on the prevomer, palatine, fifth ceratohyal and pharyngobranchials (Matsubara and Ochiai 1955; pers. obs.). These conditions probably evolved along with its specialized feeding habits. Accordingly, the presence of long canine teeth on these bones is considered as a single character.

TS 83. Coronomeckelian

0: present; 1: absent. This is absent only in *Elates*.

Outgroups. All outgroups have a coronomeckelian.

Polarity. ON = 0.

Other variations

Notch on upper tooth plate. An anteromedial notch on the upper tooth plate is seen in some platycephalids (Fig. 22C). However, it was present on the right side only in the examined *Suggrundus rodericensis* (HUMZ 13890). Moreover, intraspecific variation of the notch was reported by Matsubara and Ochiai (1955). Therefore, this character was not used in the analysis.

Suspensorium and opercular bones (Figs 23-25)

Description

The suspensorium consists of seven elements: the hyomandibular, metapterygoid, quadrate, symplectic, entopterygoid, ectopterygoid and palatine. The opercular bones include four elements: the preopercle, opercle, interopercle and subopercle.

The hyomandibular forms the dorsal portion of the suspensorium, having two condyles articulating dorsally with the neurocranium, and one articulating posteriorly with the opercle. It is connected to the metapterygoid anteriorly and the preopercle posteriorly, and bears a lateral process for the A1 muscle posteriorly. The

hyomandibular has a lateral process for the levator arcus palatini in *Platycephalus*, except *P. bassensis*, *P. longispinis* and *P. marmoratus*, and in *Neoplatycephalus* (Fig. 23A).

The metapterygoid is a rectangular bone, connected with the hyomandibular posterodorsally, and the symplectic and quadrate ventrally. It bears a prominent lamina (metapterygoid lamina, *sensu* Matsubara 1943) dorsally, supporting the levator arcus palatini dorsomedially.

The quadrate is a triangular bone with a condyle on its anteroventral corner for articulation with the anguloarticular. The former is connected with the ectopterygoid anteriorly, the metapterygoid dorsally, the preopercle posteroventrally and the symplectic dorsomedially.

The symplectic is a wedge-like bone, attached to the quadrate anterolaterally and the metapterygoid anteriorly. It has a cartilaginous cap on its anterior tip and a cartilaginous socket posteriorly for articulation with the interhyal.

The entopterygoid is a thin oval bone, with an unossified medial margin. It is sutured to the palatine anterodorsally and the ectopterygoid posteroventrally.

The ectopterygoid is a sickle-like bone, connected with the palatine anterolaterally, the entopterygoid dorsomedially and the quadrate posteriorly.

The palatine is a stout, stick-like bone, attached to the entopterygoid posteroventrally and the ectopterygoid posteromedially. It usually bears villiform and/or small canine tooth bands ventrally, but has very large, stout canine teeth in *Neoplatycephalus* (Fig. 23A) and long, slender teeth in *Ratabulus* (Fig. 23B). A facet articulating with the lateral ethmoid is present dorsally in *Platycephalus fuscus*, *P. caeruleopunctatus* and *Neoplatycephalus* (Figs 23A, 24).

The preopercle is a crescent-like bone, having a tubular structure of the preoperculo-mandibular canal along its posterior border. It bears a backward

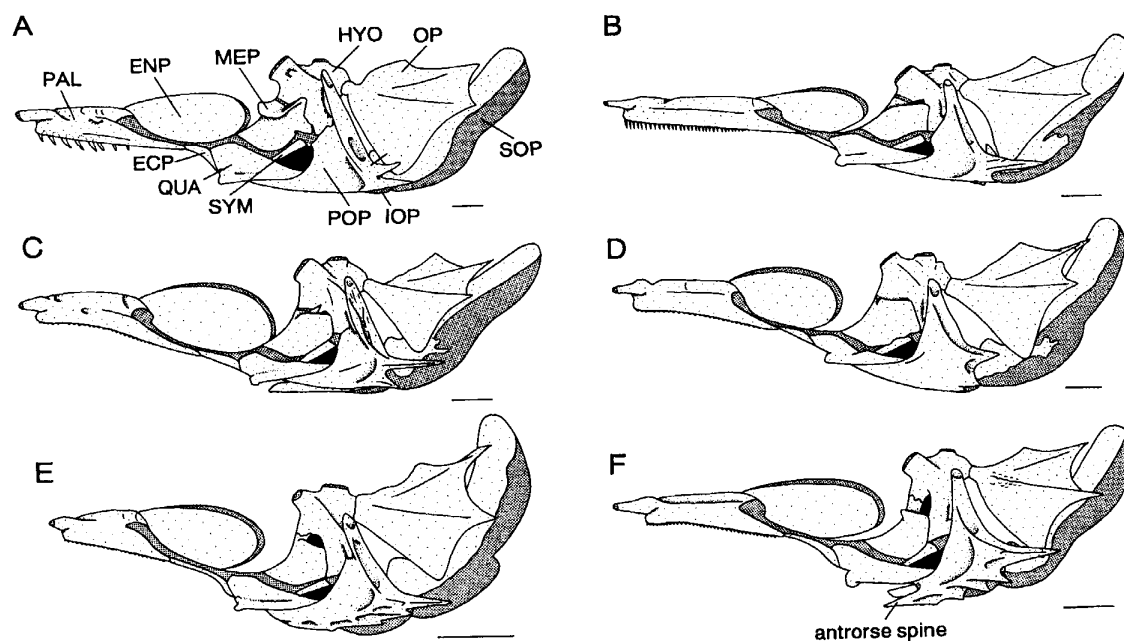


Fig. 23. Lateral aspect of suspensorium and opercular bones. A, *Neoplatycephalus richardsoni*; B, *Ratabulus megacephalus*; C, *Suggrundus rodericensis*; D, *Inegocia japonica*; E, *Onigocia macrolepis*; F, *Rogadius asper*. Scales indicate 5mm.

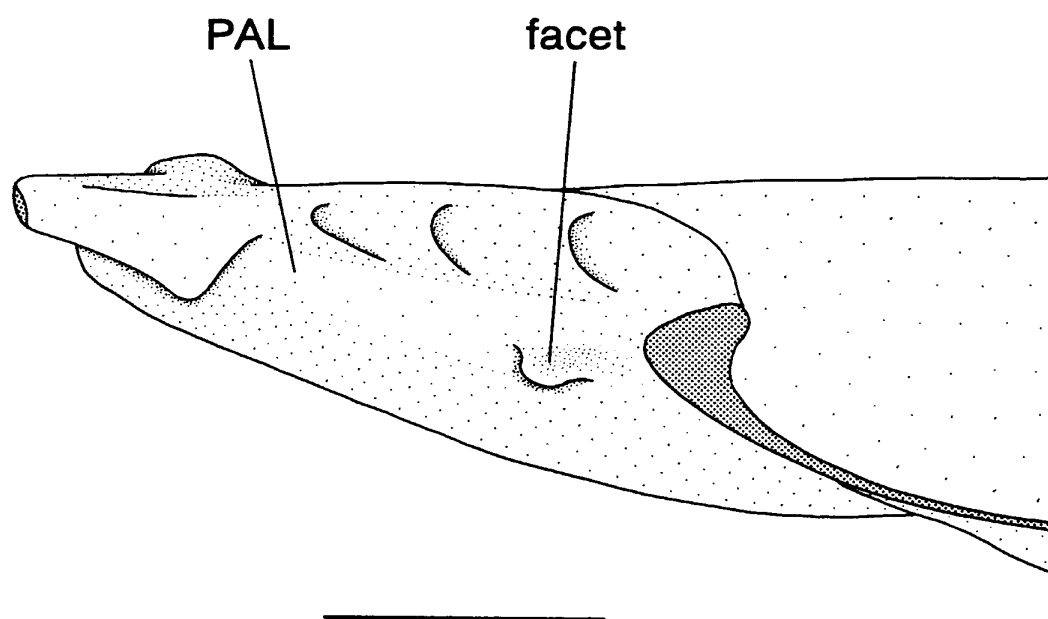


Fig. 24. Dorsal aspect of anterior part of suspensorium in *Platycephalus fuscus*. Scale indicates 5mm.

spine(s) posteriorly, but it also has a strong antrorse spine anteroventrally in *Rogadius asper* and *R. pristiger* (Fig. 23F). The tubular structure of the preoperculo-mandibular canal is continuous with those on the lower jaw (anteroventrally) and the neurocranium (dorsally). The preopercle is sutured to the hyomandibular anterodorsally and the quadrate anteroventrally.

The opercle is a thin, triangular bone, articulating with the hyomandibular anteriorly and overlapping the subopercle ventromedially. It bears three spines, the uppermost directed upward, the middle one backward and upward, and the lowermost backward. The uppermost spine is often blunt, lacking prominence, and is usually covered by skin.

The interopercle, a thin, elliptical bone (usually) with an unossified ventral margin, is situated under the inner ventral surface of the preopercle (Fig. 23). It is connected to the retroarticular anteriorly, via a strong ligament, and to the subopercle posteromedially, and is expanded posteroventrally in *Thysanophrys chiltonae*, and ventrally in *T. arenicola* and *T. otaitensis* (Fig. 25).

The subopercle is a thin, L-shaped bone, connected with the lower medial part of the opercle dorsolaterally and the posterior medial portion of the interopercle anterolaterally. Its posterior margin is not ossified.

Characters

TS 84. Teeth on palatine

0: villiform and/or small canine teeth; 1: strong, stout canine teeth. Strong, stout canine teeth are present in *Neoplatycephalus*.

Outgroups. Palatine teeth are absent in the triglids *Chelidonichthys*, *Lepidotrigla* and *Pterygotrigla*, and the peristediids, whereas villiform and/or small canine teeth are present in the other outgroups (Fig. 10).

Polarity. ON = 0.

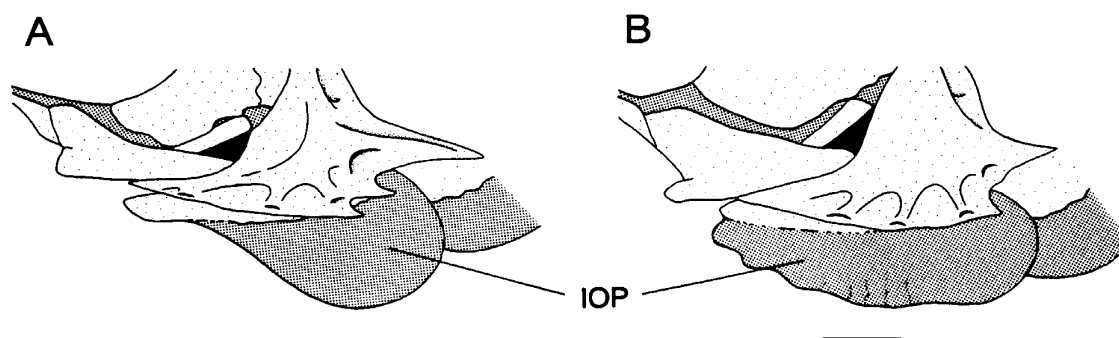


Fig. 25. Lateral aspect of interopercle. A, *Thysanophrys chiltonae*; B, *T. arenicola*. Scales indicate 5mm.

TS 85. Facet on palatine

0: absent; 1: present. A facet is found in *Platycephalus fuscus*, *P. caeruleopunctatus* and *Neoplatycephalus*.

Outgroups. A facet is absent in all outgroups, except *Hoplichthys haswelli* (Fig. 10).

Polarity. ON=0.

TS 86. Hyomandibular process for levator arcus palatini

0: absent; 1: present. A process is present in *Platycephalus fuscus*, *P. caeruleopunctatus* and *Neoplatycephalus*.

Outgroups. The process is absent in all outgroups (Fig. 10).

Polarity. ON=0.

TS 87. Antorse preopercular spine

0: absent; 1: present. The spine is present in *Rogadius asper* and *R. pristiger*.

Outgroups. All outgroups lack antorse preopercular spines (Fig. 10).

Polarity. ON=0.

TS 88. Interopercle

0: elliptical; 1: expanded posteroventrally; 2: expanded ventrally. The interopercle is expanded posteroventrally in *Thysanophrys chiltonae*, and ventrally in *T. arenicola* and *T. otaitensis*.

Outgroups. All outgroups have an elliptical interopercle, except *Parabembras*, which has a strong spine posteriorly (Fig. 10).

Polarity. ON=0 (ordered as 0-1-2).

Other variations

Number of backwardly directed spines on preopercle. The number of preopercular spines varies among the platycephalids. However, because intraspecific variation is found in at least *Sorsogona tuberculata* and *Rogadius asper*, the number of spines was not included in the analysis.

Supplemental preopercular spine. Although the preopercle has a supplemental preopercular spine in the platycephalids, except *Platycephalus*, *Neoplatycephalus*, *Elates* and *Inegocia*, intraspecific variation (presence and absence) is found in *Thysanophrys chiltonae*. Moreover, Matsubara and Ochiai (1955) pointed out that the condition varies in *Inegocia japonica*. Accordingly, this spine was not used in the analysis.

Hyoid arch (Figs 26-29)**Description**

The hyoid arch consists of seven basic elements: hypohyals (2), ceratohyal, epihyal, interhyal, branchiostegal rays (7), urohyal and basihyal.

The hypohyals, small bones situated on the anteriormost portion of the hyoid arch, comprise two (dorsal and ventral) elements. The dorsal hypohyal is sutured to the ventral hypohyal ventrally and the ceratohyal posteriorly, while its medial knob articulates with the first basibranchial. The ventral hypohyal is sutured to the dorsal hypohyal dorsally and the ceratohyal posteriorly, and is connected to the urohyal by a strong ligament.

The ceratohyal is a large, flattened bone, with slender anterior and deep posterior portions. It is connected with the hypohyals anteriorly and the epihyal posteriorly, and supports the branchiostegal rays (except the posteriormost).

The epihyal is a flattened, triangular bone, connected with the ceratohyal anteriorly and articulating with the cartilaginous ventral head of the interhyal posterodorsally. It supports the last branchiostegal ray ventrally.

The interhyal, a short, rod-like bone with cartilaginous caps on both ends, articulates with the facet on the posterior corner of the epihyal ventrally and the cartilaginous socket surrounded by the hyomandibular, preopercle and symplectic, dorsally.

Seven long, slender branchiostegal rays are suspended from the ceratohyal and epihyal and support the gill membrane.

The urohyal is a triangular bone, firmly sutured to the first basibranchial in all platycephalids. It is also firmly sutured to the second basibranchial in all platycephalids, except *Elates*, *Neoplatycephalus* and *Platycephalus*, the two bones

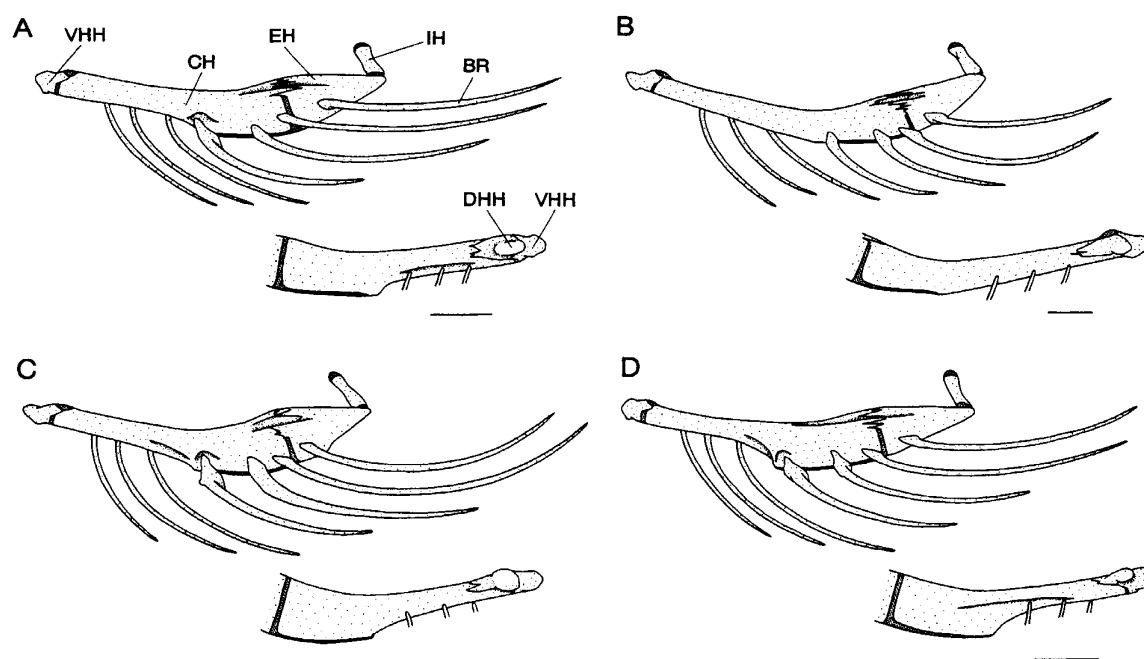


Fig. 26. Lateral (upper) and medial (lower) aspects of hyoid arch. A, *Cociella crocodila*; B, *Suggrundus rodericensis*; C, *Grammoplites scaber*; D, *Rogadius asper*. Scales indicate 5mm.

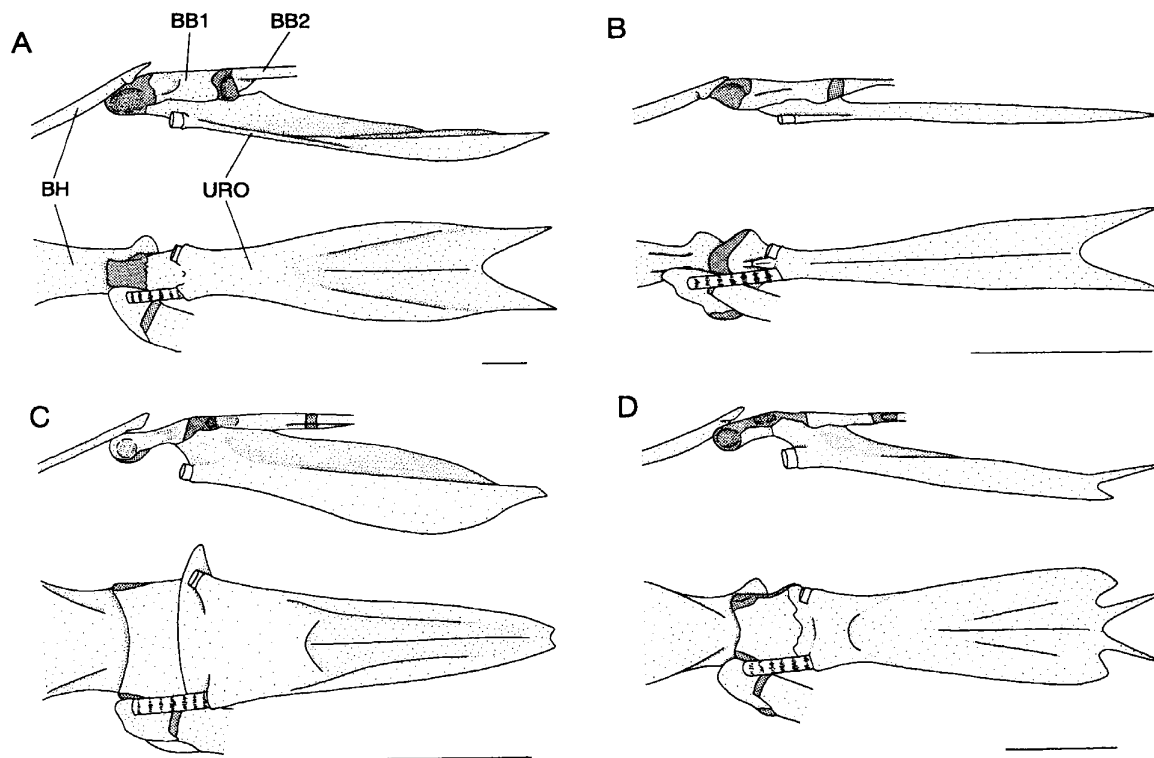


Fig. 27. Lateral (upper) and ventral (lower) aspects of urohyal. A, *Neoplatycephalus richardsoni*; B, *Elates ransonneti*; C, *Onigocia macrolepis*; D, *Rogadius asper*. Scales indicate 5mm.

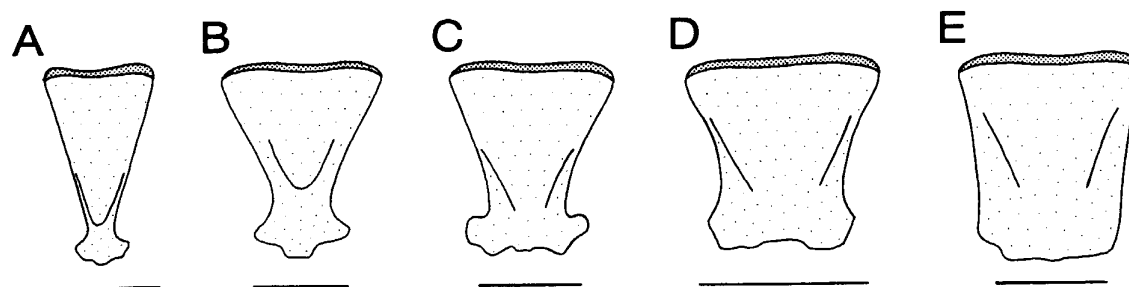


Fig. 28. Dorsal aspect of basihyal. A, *Elates ransonneti*; B, *Neoplatycephalus richardsoni*; C, *Suggrundus rodericensis*; D, *Suggrundus meerdervoortii*; E, *Thysanophrys chiltonae*. Scales indicate 5mm.

being separated in the latter by cartilage or attached loosely by a ligament (Fig. 27).

The fan-like basihyal articulates posteroventrally with the anterodorsal surface of the first basibranchial (Figs 28, 29).

Characters

TS 89. Urohyal and second basibranchial

0: separated; 1: sutured. These bones are sutured in all platycephalids, except *Platycephalus*, *Neoplatycephalus* and *Elates*.

Outgroups. They are separated in all outgroups.

Polarity. ON=0.

Other variations

Configuration of urohyal. Although the configuration of the posterior margin of the urohyal varies among platycephalids (Matsubara and Ochiai 1955; Kusaka 1974; pers. obs.), two conditions (two long and two short, and two long and four short projections) are found in *Rogadius asper*. Such variation appears to be intraspecific. Hence posterior urohyal configuration was not used in the analysis.

Configuration of basihyal. Basihyal configuration varies continuously among the platycephalids (Fig. 28). The difficulty of separating the configuration into discrete characters precluded its use in the analysis.

Branchial arch (Figs 29-30)

Description

The branchial arch consists of five elements, the lower part including the basibranchial, hypobranchial and ceratobranchial, and the upper part including the

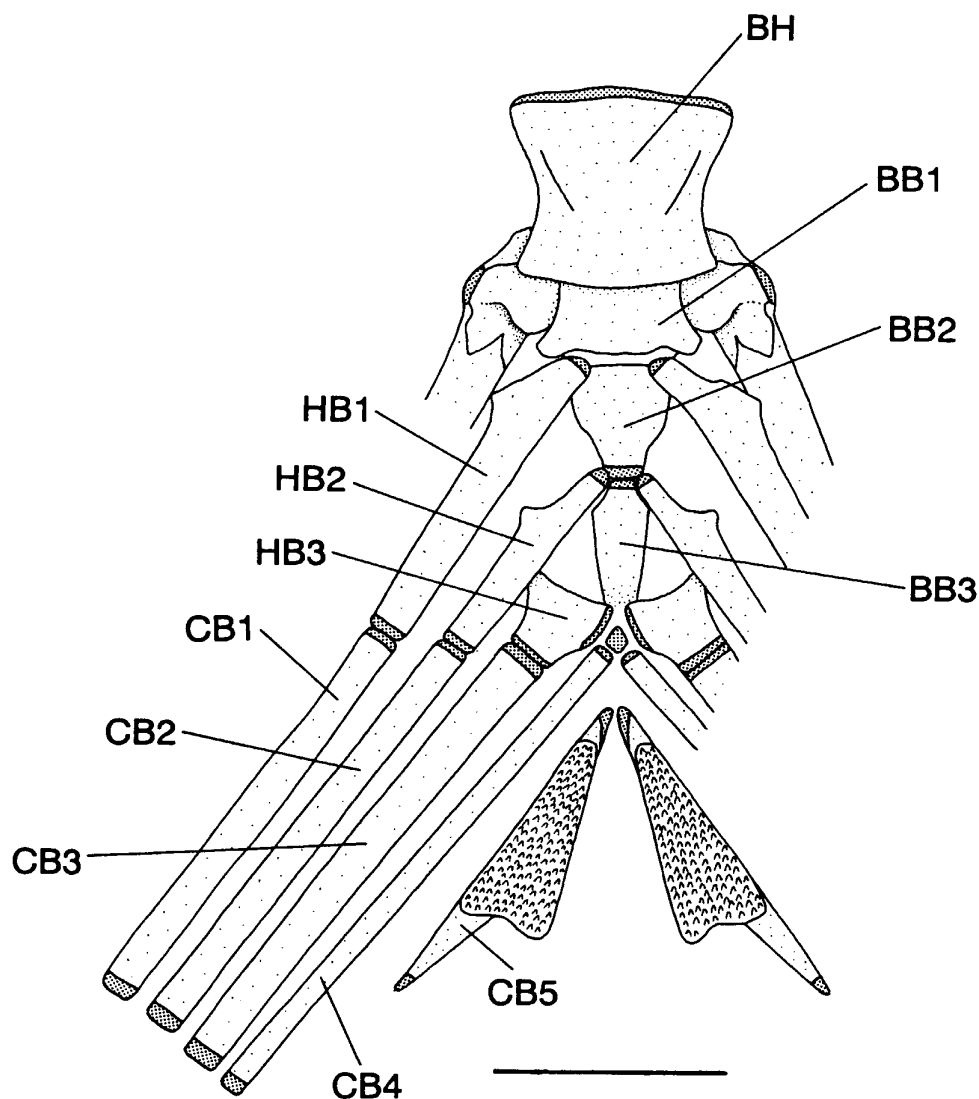


Fig. 29. Dorsal aspect of lower branchial arch of *Sorsogona tuberculata*. Scale indicates 5mm.

epibranchial and pharyngobranchial.

The basibranchials are three flattened bones, situated on the midline of the oral floor. The anteriormost (first) basibranchial is sandwiched laterally by the anterior parts of the hyoid arches and is loosely attached to the basihyal anterodorsally. The second basibranchial (on a plane between the first and third) lies between the first hypobranchials anterolaterally. The third basibranchial is sandwiched by the second and third hypobranchials anterolaterally and posterolaterally, respectively.

The hypobranchials are three paired bones, becoming progressively smaller posteriorly. The first articulates at the junction between the first and second basibranchials anteriorly and with the first ceratobranchial posteriorly, and the second at the junction between the second and third basibranchials anteriorly and with the second ceratobranchial posteriorly. The third is located between the posterior part of the third basibranchial and the anterior facet of the third ceratobranchial.

The ceratobranchials comprise four rod-like and one triangular, toothed bones. The first to third articulate with the hypohyal facets anteriorly and those of the epibranchials posteriorly. The fourth ceratobranchials oppose each other medially, being articulated with the fourth epibranchials posteriorly. The fifth ceratobranchials are in contact with each other anteromedially.

The epibranchials are four short, rod-like bones, situated between the pharyngobranchials and ceratobranchials. The second and third bear tooth plates ventrally.

The pharyngobranchials comprise three toothed and one small, toothless bones. The first is connected with the parasphenoid anteriorly and with the lower branch of the first epibranchial. The second is connected directly with the upper branch of the

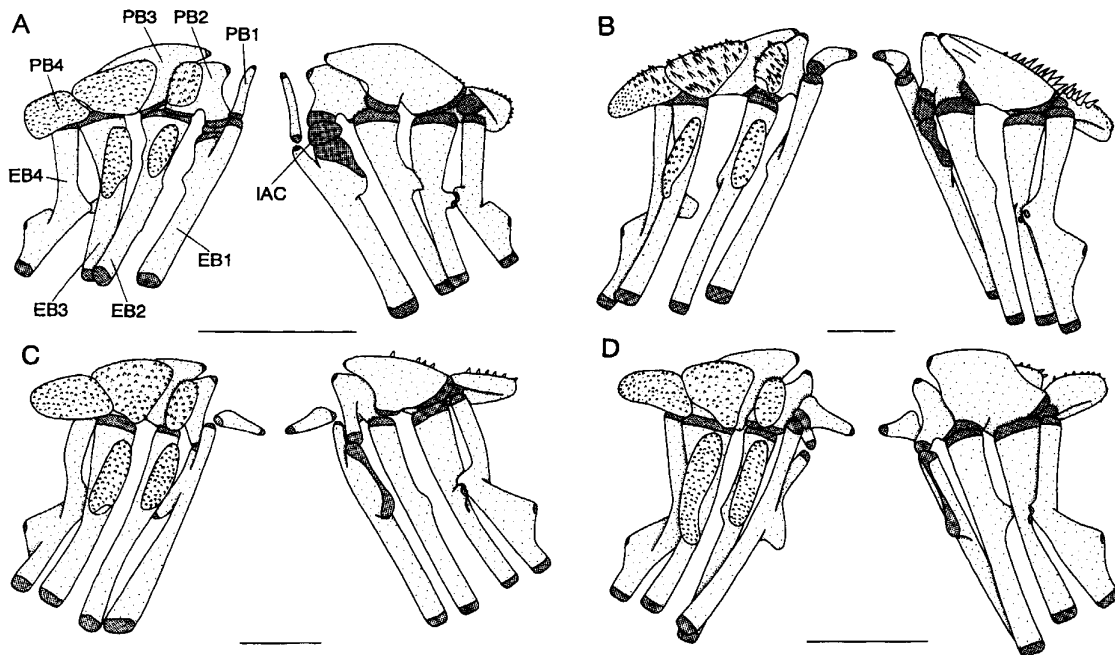


Fig. 30. Ventral (left) and dorsal (right) aspects of upper branchial arch. A, *Elates ransonneti*; B, *Ratabulus megacephalus*; C, *Suggrundus meerdervoortii*; D, *Sorsogona tuberculata*. Scales indicate 3mm.

first epibranchial, or via the interarcual cartilage (if present), and with the second epibranchial. An interarcual cartilage is absent in all platycephalids, except *Platycephalus*, *Neoplatycephalus*, *Elates*, *Ratabulus* and *Thysanophrys cirronasa* (Fig. 30). The third pharyngobranchial is attached to the second and third epibranchials, and the fourth to the fourth epibranchial.

Characters

TS 90. Interarcual cartilage

0: present; 1: absent. The cartilage is absent in all platycephalids, except *Platycephalus*, *Neoplatycephalus*, *Elates*, *Ratabulus* and *Thysanophrys cirronasa*.

Outgroups. The cartilage is present in *Peristedion*, *Plectrogenium*, *Parabembras* and *Bembras* (Fig. 7A-B, F), but is absent in the other outgroups (Fig. 7C-E).

Polarity. ON=0 or 1.

Other variations

Anterior part of first basibranchial. A large ligament, connected with the anterior region of the first basibranchial in *Elates*, *Platycephalus*, *Neoplatycephalus*, *Ratabulus diversidens*, *Sorsogona nigripinna*, *S. prionota*, *Suggrundus macracanthus*, *S. rodericensis*, *S. meerdervoortii*, *Cymbacephalus beauforti*, *Grammoplites suppositus* and *Papilloculiceps*, was not found in other platycephalids or the outgroups, and can be regarded as an apomorphic character. However, since intraspecific variation is found in *Ratabulus megacephalus* (ligament either exposed or covered by first basibranchial anteriorly), this character was not used in the analysis.

Tooth plate on third basibranchial. In *Sorsogona nigripinna*, a tooth plate is present on the third basibranchial. Although the character is apomorphic, since the plate is absent in all outgroups, it was not used because of intraspecific variation in *Suggrundus macracanthus*.

Pectoral girdle (Fig. 31)

Description

The pectoral girdle is comprised of the supratemporal, posttemporal, supracleithrum, cleithrum, postcleithrum, scapula, coracoid and actinosts.

The supratemporal is a plate-like bone, situated on the posttemporal. It bears a cephalic sensory canal continuous with that on the pterotic, parietal and posttemporal.

The posttemporal is a forked bone with its ventral limb connected to the intercalar ventrally. It is also connected with the pterotic dorsolaterally and the epiotic dorsomedially.

The supracleithrum is a plate-like bone, bearing a sensory tube continuous with that on the posttemporal and anteriormost lateral line scale. It is connected with the posttemporal anterodorsally, the lateral line scale posterodorsally and the cleithrum medially. Baudelot's ligament connects the medial surface of this bone to the neurocranium.

The cleithrum is the largest bone in the pectoral girdle and bears a lateral wing-like structure. It meets the supracleithrum dorsolaterally, postcleithrum posteromedially if present, scapula posterodorsally and coracoid posteroventrally.

The postcleithra comprise two usually thin, leaf-like bones. The upper element meets the cleithrum dorsolaterally and is the lower element ventromedially.

The scapula is a rectangular bone, having a large scapular foramen anteriorly. It

is sutured to the cleithrum anteriorly, and is connected with two upper actinosts posteriorly and the coracoid ventrally, via a narrow cartilaginous band.

The coracoid is a strongly curved bone, bearing an antorse arm ventrally. The latter is connected with the anteromedial part of the cleithrum. This bone is also connected with the scapula dorsally and the lower two actinosts posteriorly.

Four thick, plate-like actinosts support the pectoral fin rays posteriorly and are short and deep (Fig. 31). The upper two elements are attached to the scapula and the lower two to the coracoid.

Characters

No derived characters that could be used in the analysis were found.

Other variations

Number of postcleithra. The number of postcleithra varies in the platycephalids,

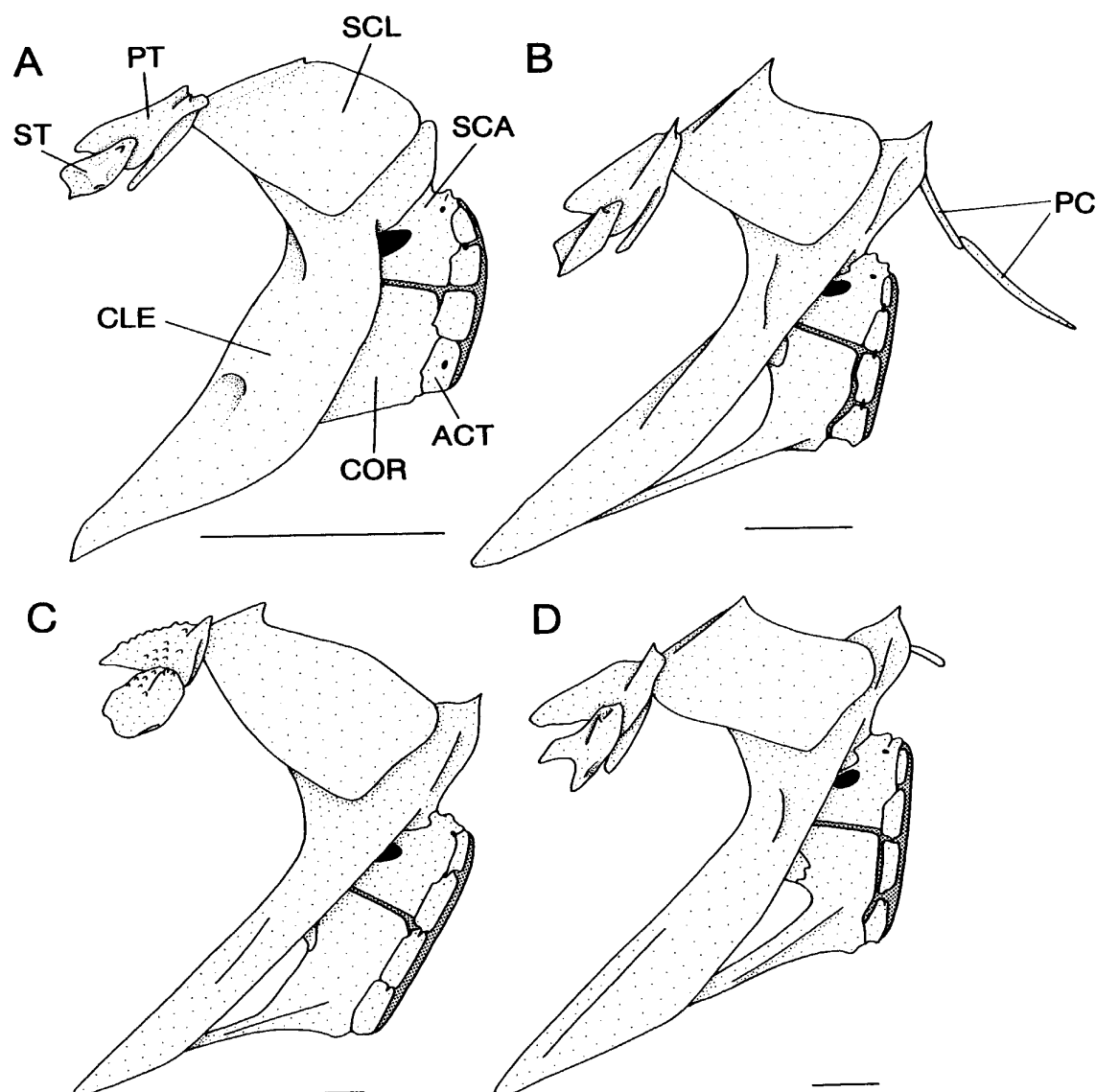


Fig. 31. Lateral aspect of pectoral girdle. A, *Elates ransonneti*; B, *Ratabulus megacephalus*; C, *Sorsogona tuberculata*; D, *Cociella crocodila*. Scales indicates 5mm.

but could not be used in the analysis, because of intraspecific variation found in at least *Suggrundus meerdervoortii* and *Thysanophrys chiltonae*.

Pelvic girdle (Fig. 32)

Description

The pelvic girdle comprises a pair of L-shaped pelvic bones, forming a large intermediate space. Each anterior tip has a small cartilaginous cap. The posterodorsal portion bears a distinct fossa (posterior pelvic fossa) serving the infracarinalis medius. The posteromedial ends of the pelvic bones are separated from each other.

Characters

No derived characters that could be used in the analysis were found.

Other variations

Configuration of postpelvic process. Matsubara and Ochiai (1955) noted the configuration of the postpelvic process (simple or branched into two or three) in the platycephalids. Intraspecific variation occurs in *Suggrundus rodericensis* (simple and bifid). Moreover, the process, which is bifid in *Ratabulus megacephalus* according to Matsubara and Ochiai (1955), has three branches in the present specimens.

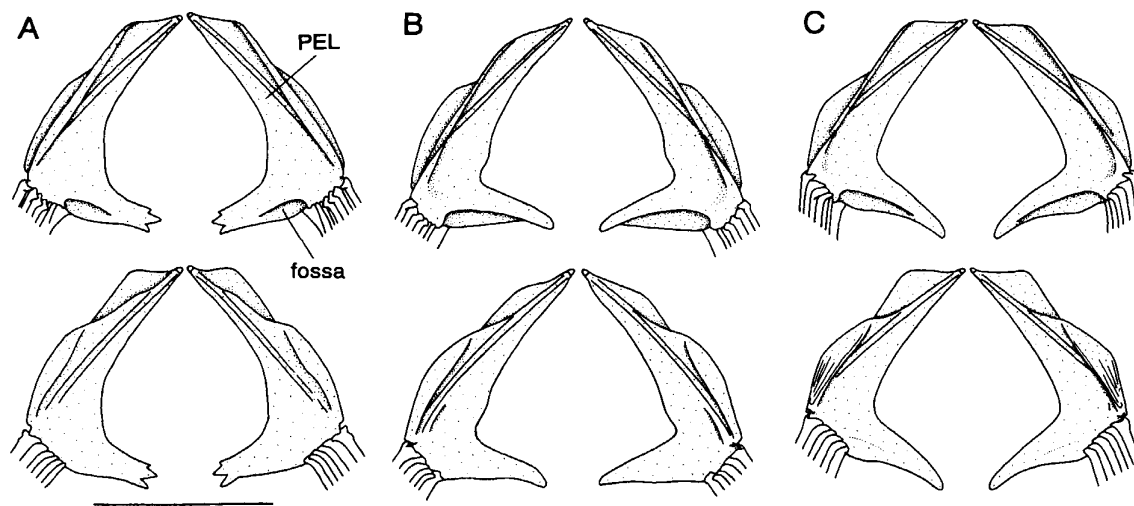


Fig. 32. Dorsal (upper) and ventral (lower) aspects of pelvic girdle. A, *Elates ransonneti*; B, *Cociella crocodila*; C, *Grammoplites scaber*. Scales indicate 5mm.

Axial skeleton and median fin supports (Figs 33, 34)

Description

The axial skeleton is comprised of the vertebrae, pleural ribs (lower) and epineurals (upper) (*sensu* Patterson and Johnson 1995). The median fin supports consist of the proximal and distal pterygiophores and stays. Predorsal and medial pterygiophores are absent.

Axial skeleton. The vertebrae include the abdominal and caudal elements. The anterior 12-14 vertebrae have the epineurals on their lateral aspects or parapophyses. Neural arches, bearing a dorsal spine, are present. The caudal vertebrae each bear a hemal arch and spine.

The epineurals are slender bones, attached to the vertebrae or parapophyses

(Fig. 33A).

Three to six long, slender pleural ribs are suspended from the ventral face of the epineural ribs, except from the first two (Fig. 33A).

Medial fin supports. The proximal pterygiophores are leaf-like bones, supporting the dorsal and anal fin rays. They are inserted into the interneural and interhemal

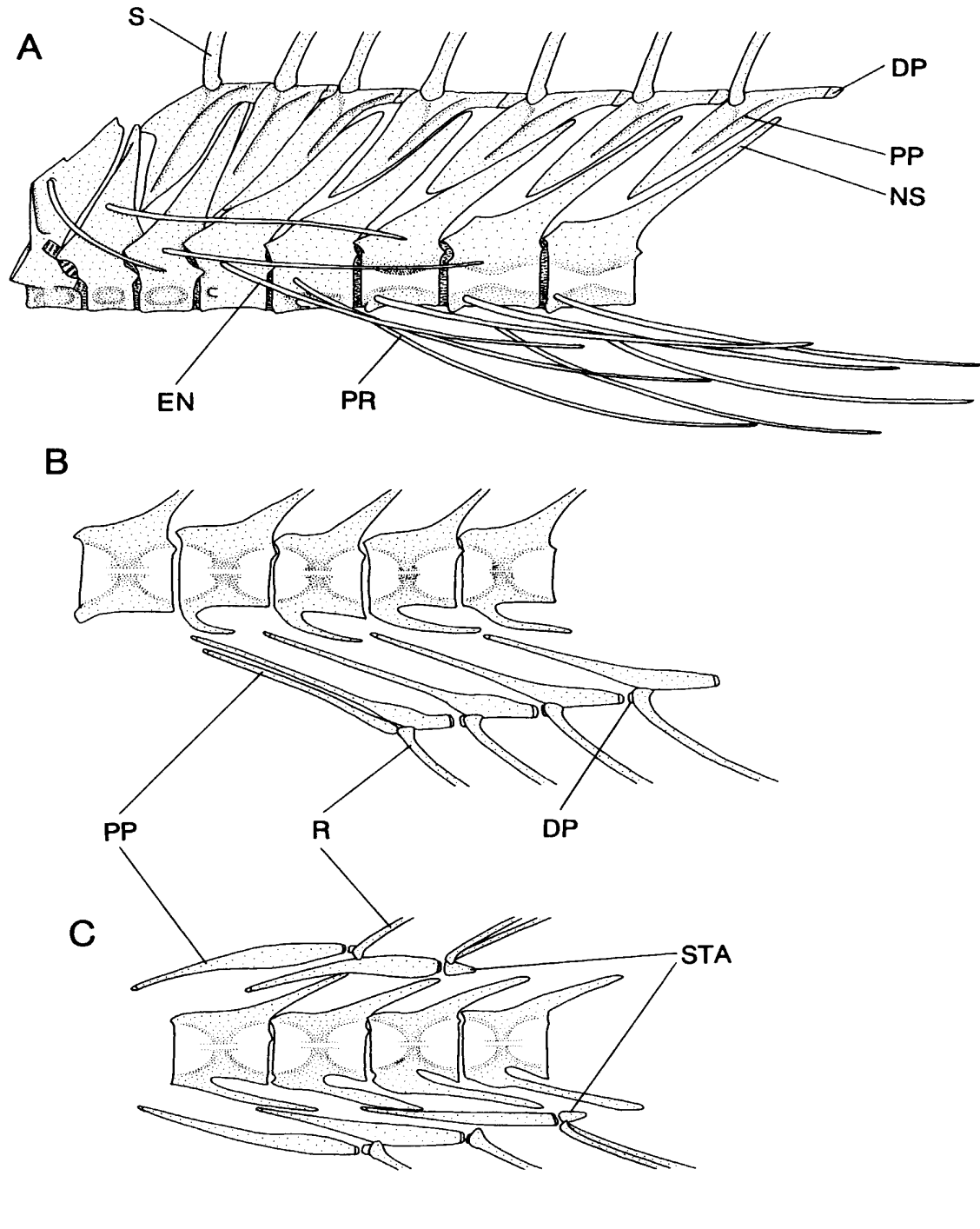


Fig. 33. Lateral aspect of anterior (A), middle (B) and posterior (C) vertebrae and associated bones in *Rogadius asper*. Scale indicates 5mm.

spaces, usually singly. The first dorsal proximal pterygiophore is inserted into the space between the second and third neural spines, and the second and third are inserted into the space between the third and fourth neural spines. Although the first proximal pterygiophore usually bears two spines in the scorpaeniforms (Fig. 34A), the first spine on the first dorsal proximal pterygiophore is absent in all platycephalids (Fig. 34B-D). The second spine is usually long (Fig. 34B), whereas it is absent in *Neoplatycephalus*, *Elates* and *Platycephalus* (Fig. 34D), except *P. fuscus*, which have a rudimentary spine (Fig. 34C). The second proximal pterygiophore bears a long spine in all platycephalids (Fig. 34B), except *Platycephalus*, *Neoplatycephalus* and *Elates*, which have a very short spine (Fig. 34C, D). The first anal proximal pterygiophore lacks rays, there being one on each of the others.

The distal pterygiophores are located on the posterior tip of each of the proximal pterygiophores, except the last dorsal and anal proximal pterygiophores, and support the base of the fin rays. The distals, supporting the spines, are small plate-like bones, sutured to the anterior proximal pterygiophore. The bones supporting the soft rays are paired, attached to the posterior tip of the anterior proximal pterygiophores.

The stay is a small, plate-like bone, situated on the posterior tip of the last dorsal and anal proximal pterygiophores.

Characters

TS 91. Second spine on first dorsal proximal pterygiophore

0: long; 1: rudimentary; 2: absent. It is rudimentary in *Platycephalus fuscus*, and absent in *Neoplatycephalus*, *Elates* and all other *Platycephalus*.

Outgroups. All outgroups have a long second spine (Fig. 34A).

Polarity. ON=0 (unordered).

TS 92. Spine on second dorsal proximal pterygiophore

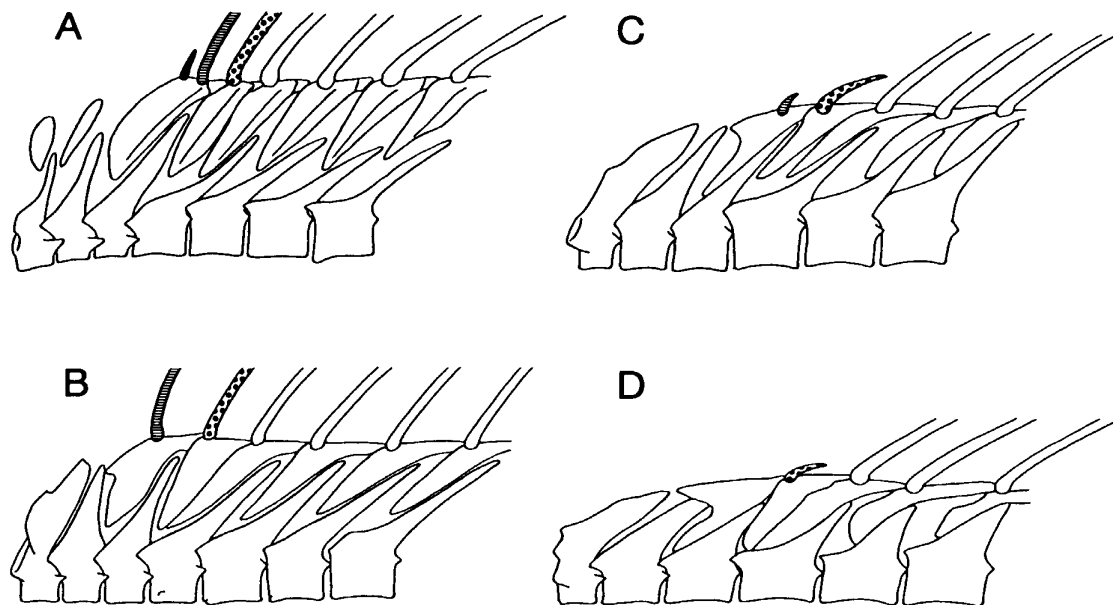


Fig. 34. Diagrammatic illustration of anterior vertebrae and associated bones. A, *Parabembras curta* (outgroup); B, *Rogadius asper*; C, *Platycephalus fuscus*; D, *Elates ransonneti*. First spine of first proximal pterygiophore black, second spine of first proximal pterygiophore striped and spine of second proximal pterygiophore dotted.

0: long; 1: very short. The spine is very short in *Platycephalus*, *Neoplatycephalus* and *Elates*.

Outgroups. All outgroups have a long spine (Fig. 34A).

Polarity. ON=0.

Other variations

Configuration of first neural spine. Shinohara (1994) selected a plate-like first neural spine as a derived character for his analysis of scorpaeniform relationships. The configuration of this spine changes continuously among the platycephalids examined in this study so it was impossible to recognize discrete characters.

Caudal skeleton (Fig. 35)

Description

The caudal skeleton consists of the hypurals, parhypural, uroneural, epurals and urostyle, plus hemal spines on the second and third preural centra.

The hypurals constitute five plate-like bones in all outgroups, except triglids, peristediids and hoplichthyids; they are situated on the posterior portion of the urostyle and support the caudal fin rays. Three elements occur in the upper caudal lobe, two in the lower lobe. The lower two of the upper elements (third and fourth hypurals) are fused in all platycephalids, except *Ratabulus*. The lower elements (first and second hypurals) are fused in all platycephalids.

The parhypural is a plate-like bone, located under the lowermost hypural.

The uroneural is a rod-like bone, lying above the urostyle and uppermost hypural. A second uroneural is present in only *Ratabulus* (Fig. 35A).

The epurals are three rod-like bones, located above the uroneural.

The urostyle, a triangular bone, free from the other caudal skeleton elements, articulates anteriorly with second preural centrum.

The hemal spines are slender, plate-like bones, those on the second and third preural centra usually being free from the latter. In *Elates*, the third preural centrum and associated spine are fused (Fig. 35E).

Characters

TS 93. Second uroneural

0: absent; 1: present. A second uroneural is present only in *Ratabulus*.

Outgroups. None of the outgroups possess a second uroneural.

Polarity. ON=0.

TS 94. Hemal spine and third preural centrum

0: separated; 1: fused. These are fused only in *Elates*.

Outgroups. Of the outgroups, only hoplichthyids and peristediids have the hemal spine and third preural centrum fused.

Polarity. ON=0.

Other variations

Number of hypural plates. The number of hypural plates varies among platycephalids, being four (third and fourth fused) in *Ratabulus* and three (first and second, and third and fourth fused, respectively) in the others. Nevertheless, this variation was not used in the analysis, owing to the third and fourth hypurals being partially fused (anteriorly) in one of the outgroups (*Prionotus*).

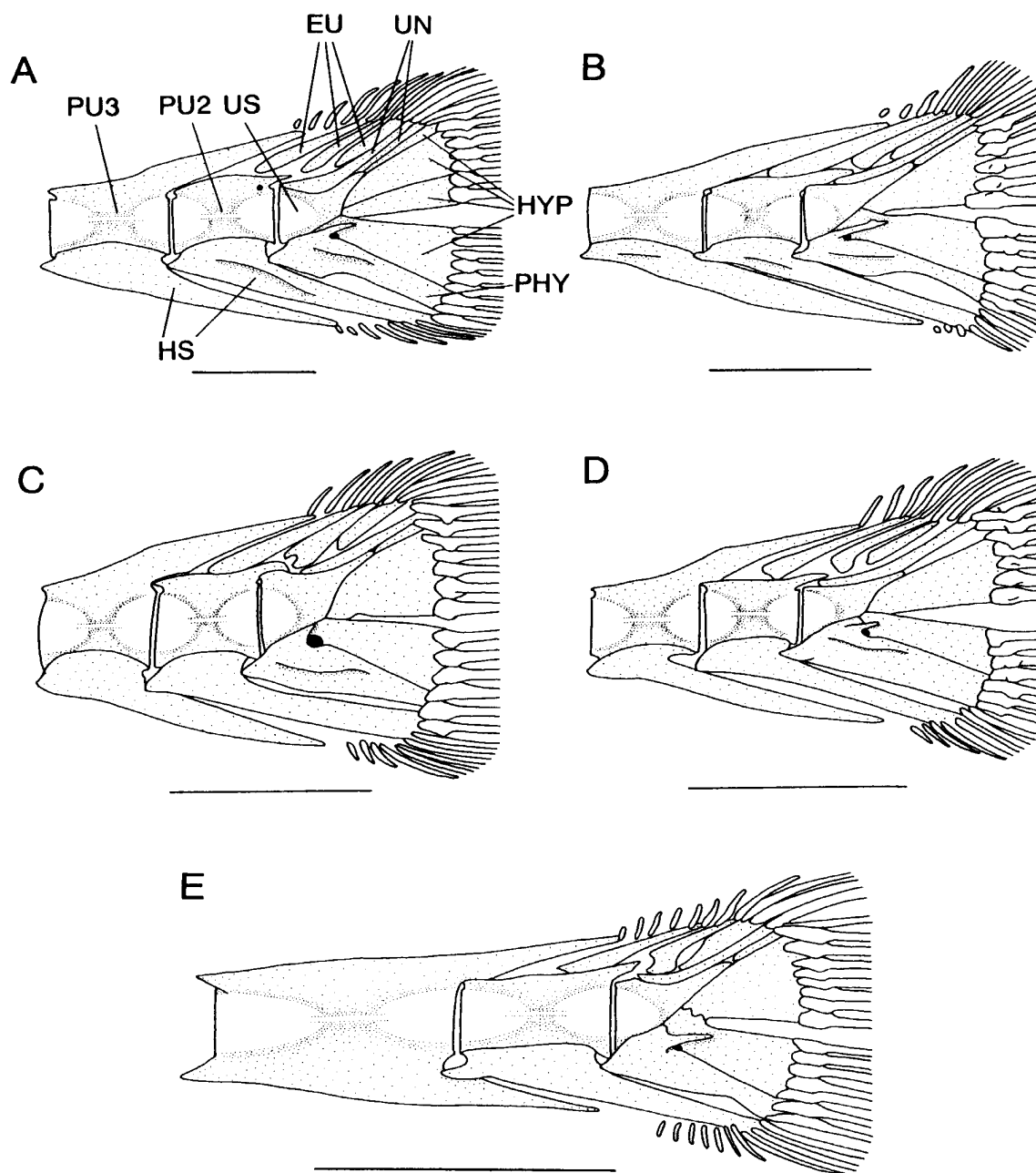


Fig. 35. Lateral aspect of caudal skeleton. A, *Ratabulus megacephalus*; B, *Thysanophrys chiltonae*; C, *Rogadius asper*; D, *Suggrundus meerdervoortii*; E, *Elates ransonneti*. Scales indicate 5mm.

II. Myology

Cheek muscle (Figs 36-39)

Description

The cheek muscle consists only of the adductor mandibulae, a large muscle comprising four sections: A1, A2, A3 and Aw. Section A1 overlies the dorsolateral part of A2, having originated from the preopercle and lateral process of

hyomandibular, and being inserted onto the ligamentum primordium. It is connected with the posterior aspect of the premaxillary condyle via a long tendon (Figs 36, 38-39). Section A2, the largest of the group, is not well separated from A3 (Figs 36, 37). It originates from the preopercle, metapterygoid, symplectic, quadrate and lateral process of hyomandibular, and is inserted onto the anguloarticular. Section A3 originates mainly from the metapterygoid and is inserted onto Aw (Fig. 37). Aw lies on the medial surface of the lower jaw, being connected with the medial aspect of the quadrate by a strong tendon (Fig. 37).

Characters

No derived characters suitable for analysis were recognized.

Other variations

None.

Cephalic muscles between neurocranium and suspensorium-opercular bones (Figs 36, 38-39)

Description

The cephalic muscles in this region consist of the levator arcus palatini, adductor

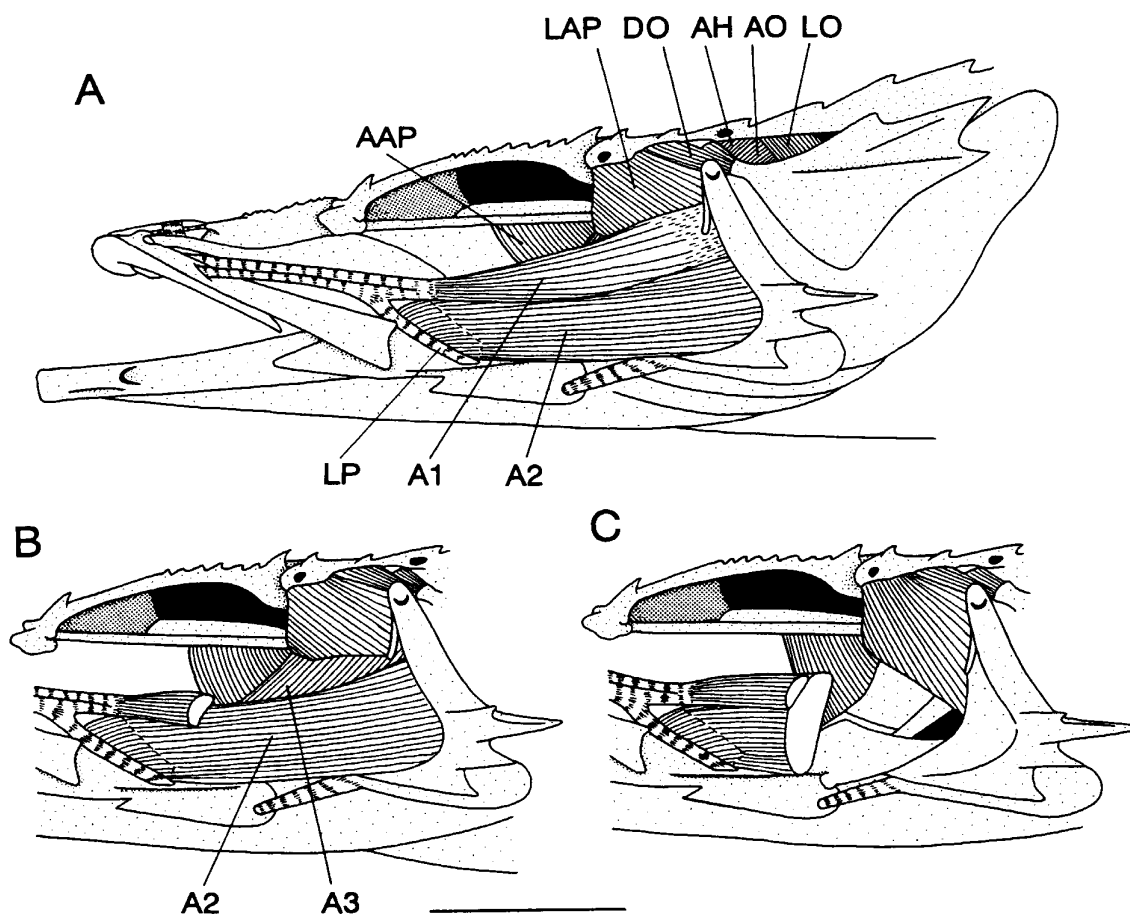


Fig. 36. Lateral aspect of cheek and other cephalic muscles in *Suggrundus meerdervoortii*. A, superficial aspect; B, lateral aspect after removal of A1; C, lateral aspect after removal of A2-3. Scale indicates 5mm.

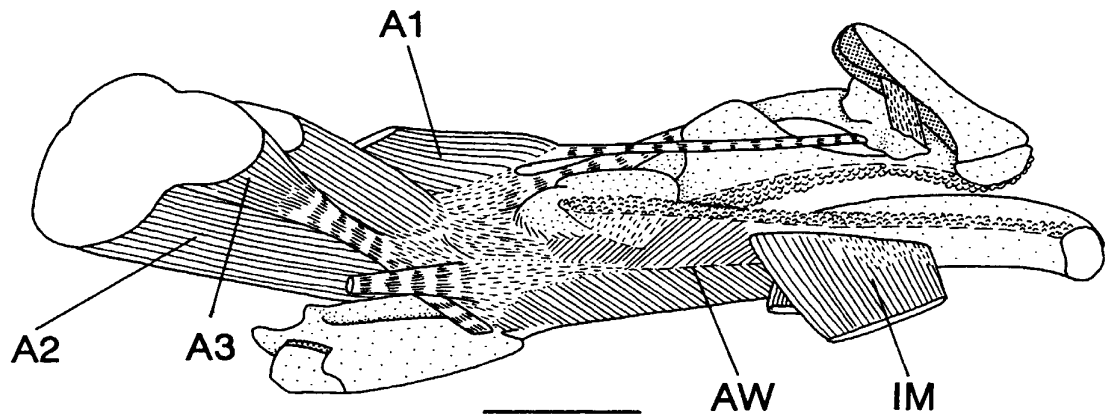


Fig. 37. Medial aspect of cheek muscles and both jaws in *Thysanophrys arenicola*. Scale indicates 5mm.

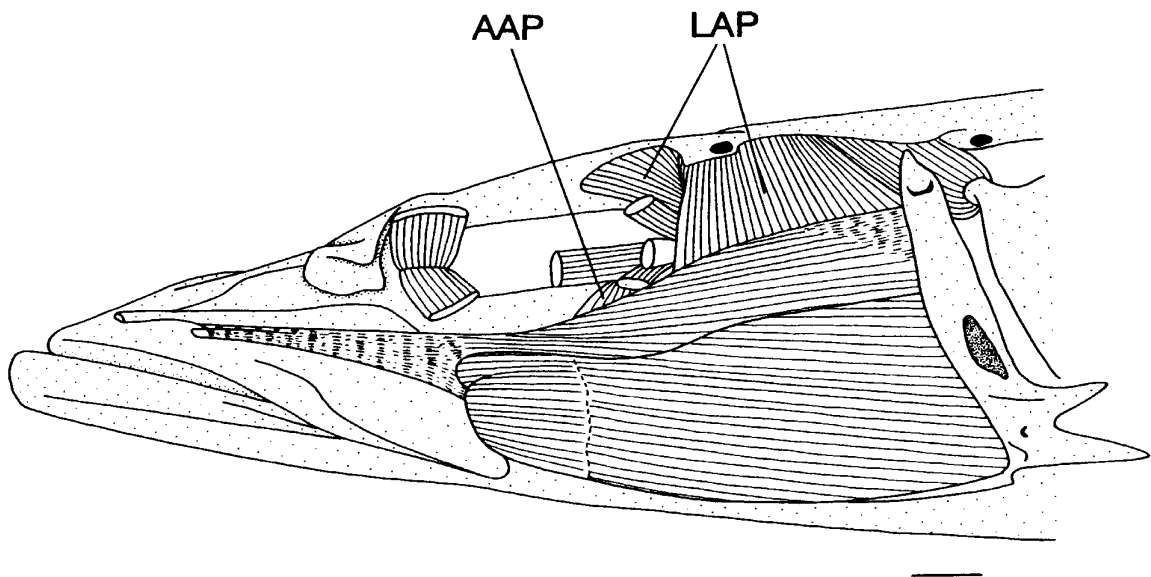


Fig. 38. Lateral aspect of cheek and other cephalic muscles in *Neoplatycephalus richardsoni*. Scale indicates 5mm.

arcus palatini, dilatator operculi, adductor operculi, adductor hyomandibular and levator operculi.

The levator arcus palatini is situated in the posterodorsal region of the suspensorium. It originates from the sphenotic and is inserted onto the preopercle, hyomandibular and metapterygoid (Figs 36, 39). This muscle also extends to the pterosphenoid and frontal in *Platycephalus fuscus* and *Neoplatycephalus* (Fig. 38).

The adductor arcus palatini, occupying the lower and posterior regions of the orbit, connects the parasphenoid with the entopterygoid, hyomandibular and metapterygoid (Figs 36, 38), and also extends to the pterosphenoid and frontal in

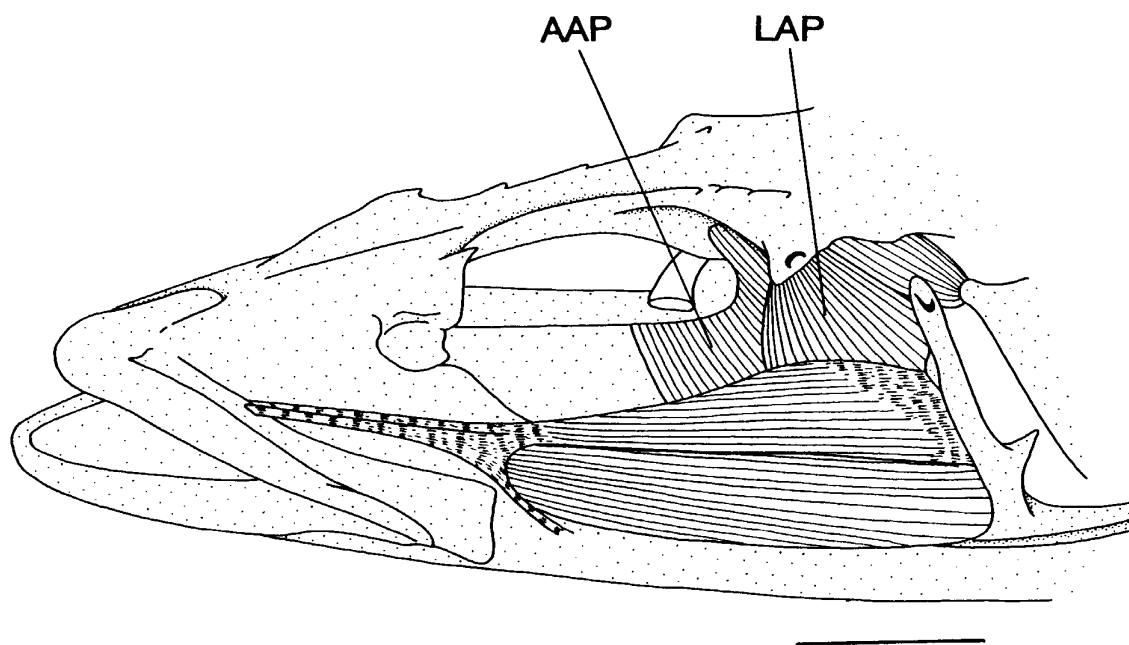


Fig. 39. Dorsolateral aspect of cheek and other cephalic muscles in *Platycephalus longispinis*. Scale indicates 5mm.

Platycephalus caeruleopunctatus, *P. bassensis*, *P. longispinis*, *P. marmoratus* and *Elates* (Fig. 39).

The dilatator operculi originates from the dorsolateral fossa of the neurocranium (just above the socket for articulation with the anterior condyle of the hyomandibular) and from the hyomandibular, and is inserted onto the anterior corner of the opercle.

The adductor operculi connects the posteroventral surface of the neurocranium with the anteromedial aspect of the opercle.

The adductor hyomandibular, adjoining the adductor operculi posteriorly, originates from the posteroventral surface of the neurocranium and is inserted onto the medial surface of the posterodorsal process of the hyomandibular.

The levator operculi, a thin, membranous muscle, originates from the posterolateral border of the pterotic and is inserted onto the upper border of the opercle.

Characters

TS 95. Muscle extending to pterosphenoid and frontal

0: none; 1: adductor arcus palatini; 2: levator arcus palatini. The adductor arcus palatini extends to the pterosphenoid and frontal in *Platycephalus caeruleopunctatus*, *P. bassensis*, *P. longispinis*, *P. marmoratus* and *Elates*, and the levator arcus palatini in *Platycephalus fuscus* and *Neoplatycephalus*.

Outgroups. No muscles extend to the pterosphenoid and frontal in the outgroups.

Polarity. ON=0 (unordered).

Other variations

None.

Ventral muscles of head (Figs 40-42)**Description**

The ventral head muscles usually comprise the intermandibularis, protractor hyoidei, hyohyoidei abductores and hyohyoidei adductores. The sternohyoideus is also described in this section.

The intermandibularis is a membranous muscle, lying between the left and right dentaries.

The protractor hyoidei is a robust muscle, originating from the anteromedial portion of the dentary via a short tendon. It is inserted onto the posterolateral surface of the ceratohyal.

The hyohyoidei abductores comprises two sections, section 1 originating from the anteroventral part of the ceratohyal and being inserted onto the proximal part of the branchiostegal rays (Fig. 40), and section 2 from the anterior part of the hyoid arch onto the first branchiostegal ray on the opposite side. These muscles cross each other, the right muscle passing medially to the left (Fig. 40).

The hyohyoidei adductores are sheet-like muscles, connecting the branchiostegal rays with the medial aspect of the opercle (Fig. 41).

The sternohyoideus, a very robust muscle, originates from the anterior portion of the pectoral girdle and is inserted onto the both the lateral and ventral aspects of the urohyal (Fig. 42).

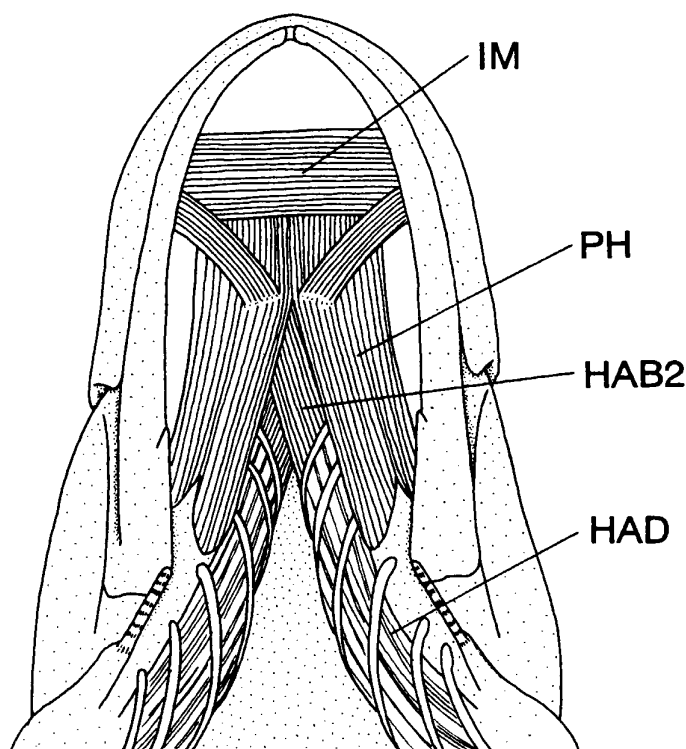
Characters

Fig. 40. Ventral aspect of ventral muscles of head in *Thysanophrys chiltonae*. Scale indicates 3mm.

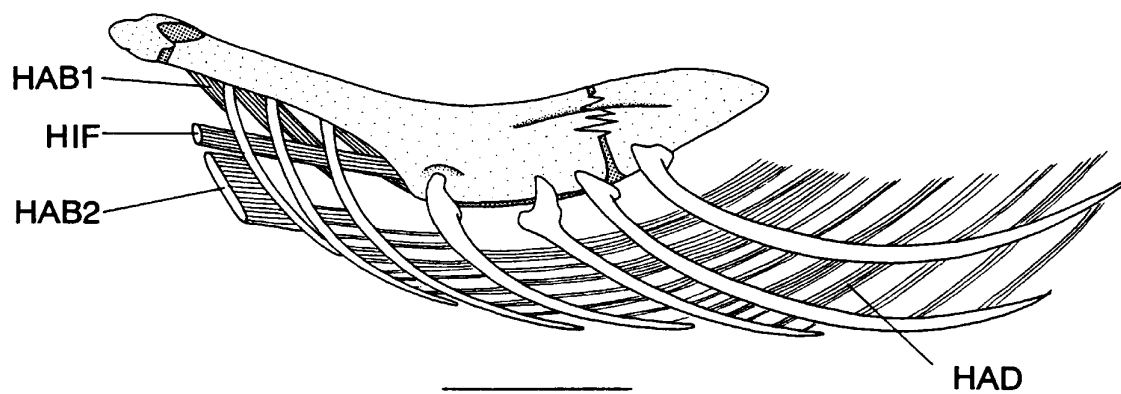


Fig. 41. Lateral aspect of ventral muscles of head in *Onigocia macrolepis*. Scale indicates 5mm.

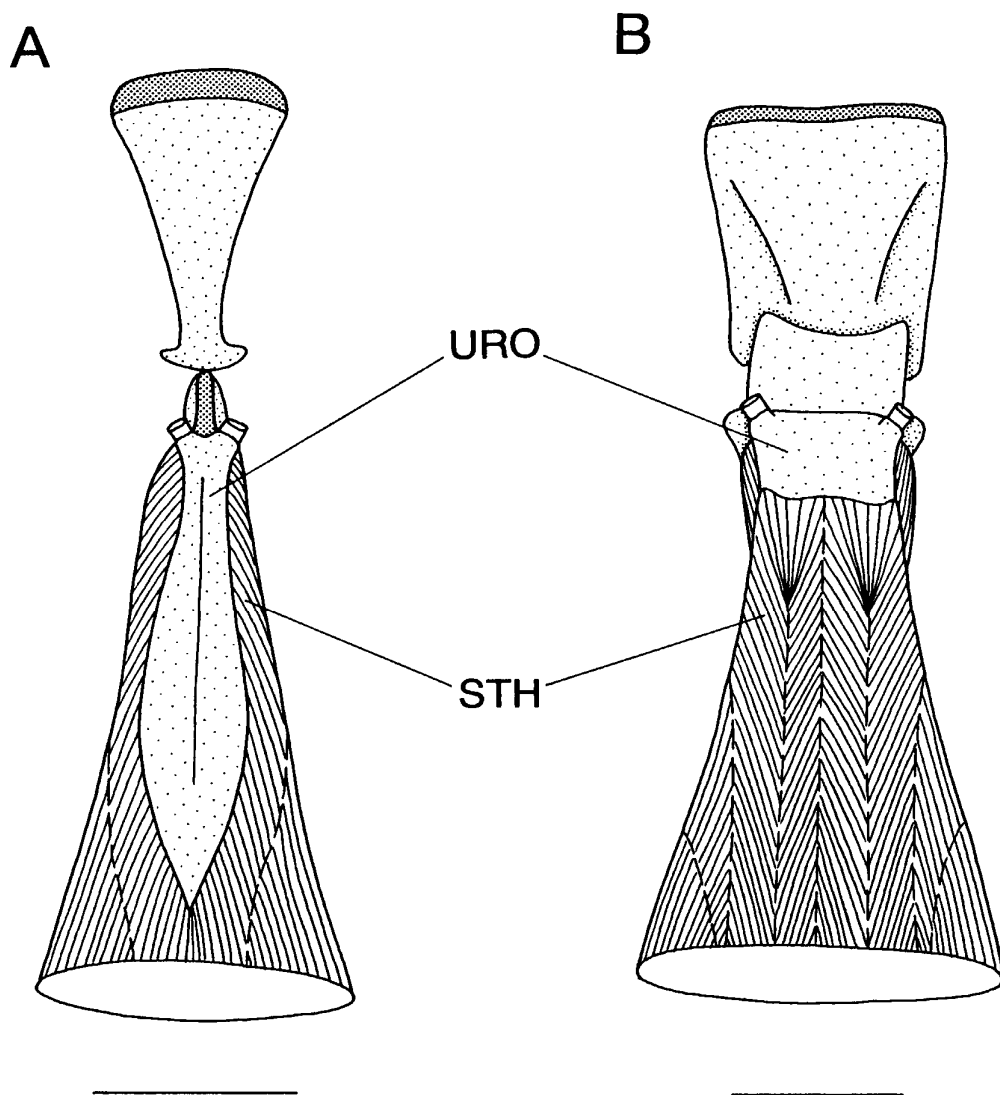


Fig. 42. Ventral aspect of sternohyoideus. A, *Parabembras curta* (outgroup); B, *Thysanophrys chiltonae*. Scale indicates 5mm.

No derived characters suitable for analysis were recognized.

Other variations

Hyohyoides inferioris. The hyohyoides inferioris is found in some platycephalids (*Ratabulus*, *Rogadius*, except *R. patriciae*, *Sorsogona prionota*, *Suggrundus cooperi*, *Thysanophrys armata*, *T. chiltonae*, *T. otaitensis*, *Grammoplites gruveli*, *G. scaber*, *Inegocia japonica*, *Neoplatycephalus richardsoni*, *Onigocia* and *Papilloculiceps*) (Fig. 41), but is absent in others. However, its variable presence or absence in *Suggrundus meerdervoortii* and *S. rodericensis* precluded use of this muscle for analysis.

Branchial muscles (Fig. 43)

Description

The branchial muscles consist of the levator externus, levator internus, levator posterior, transversus dorsalis, obliquus dorsalis, retractor dorsalis, rectus communis, pharyngoclavicularis, rectus ventralis, obliquus ventralis, transversus ventralis, sphincter oesophagi and obliquus posterior.

The levator externus usually consists of four elements, originating from the prootic and pterotic, in the latter case just below the fossa for the hyomandibular articulation, and being inserted onto the dorsal aspect of each epibranchial.

The levator internus, comprising two elements, originates just medially to the origin of the levator externus. The anterior element is inserted onto the dorsal surface of the second pharyngobranchial (and anterior border of the third), and the posterior element onto the dorsal surface of the third pharyngobranchial.

The levator posterior is a very slender muscle bundle connecting the posteroventral corner of the cranium with the posterodorsal region of the fourth epibranchial.

The transversus dorsalis consists of two elements, the transversus dorsalis anterior and posterior. The former is located on the anterodorsal portion of the upper gill arch and is unbranched laterally (Fig. 43A). The transversus dorsalis posterior interconnects the third epibranchial and third pharyngobranchial of each side.

The obliquus dorsalis originates from the third pharyngobranchial and is inserted onto the third and fourth epibranchials.

The retractor dorsalis is a thick muscle, connecting the third and fourth pharyngobranchials with the ventrolateral face of the anterior abdominal vertebrae.

The rectus communis originates from the dorsal process of the urohyal and is inserted onto the fifth ceratobranchial via a tendon.

The pharyngoclavicularis, comprising two elements, externus and internus, connects the fifth ceratobranchial with the cleithrum. The externus origin is sandwiched by the posterior portion of the sternohyoideus.

The rectus ventralis interconnects the third hypobranchial and fourth ceratobranchial.

The obliquus ventralis, comprising three muscles, connects the first to third hypobranchials with the first to third ceratobranchials, respectively.

The transversus ventralis consists of two elements, the transversus ventralis anterior and posterior, connecting the fourth and fifth ceratobranchials, respectively. The posterodorsal region of the anterior element is overlapped by the anteroventral region of the posterior element (Fig. 43B).

The sphincter oesophagi encircles the esophagus in the posterior region of the

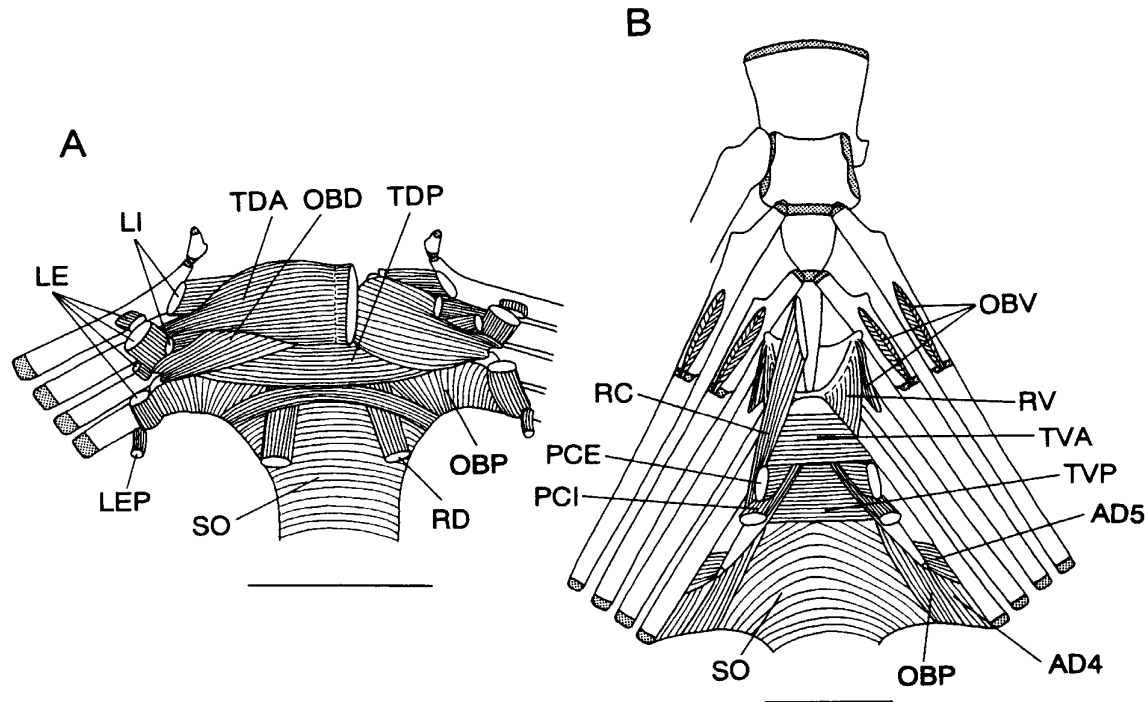


Fig. 43. Branchial muscles of *Sorsogona tuberculata*. A, dorsal aspect of muscles serving upper branchial arches; B, ventral aspect of muscles serving lower branchial arches. Scales indicate 5mm.

branchial arch.

The obliquus posterior connects the fourth epibranchial with the fifth ceratobranchial.

The adductor comprises two elements, adductor 4 and 5, interconnecting the fourth epibranchial and fourth ceratobranchial, and fourth and fifth ceratobranchials, respectively. Other elements (adductor 1-3) are absent.

Characters

No derived characters suitable for analysis were recognized.

Other variations

Third levator externus. The third levator externus is absent in *Platycephalus marmoratus*, *Sorsogona prionota*, *Suggrundus meerdervoortii*, *Inegocia japonica*, *Papilloculiceps longiceps*, *Cymbacephalus beauforti* and *C. staigeri* among Platycephalidae. Although absence of the muscle is an apomorphic character, owing to its presence in all outgroups, except hoplichthyids, it was not included in the analysis, since it was present on the right side only in a specimen of *Suggrundus jugosus* (AMS I.20845-001).

Pectoral fin muscles (Figs 44, 45)

Description

Pectoral fin muscles, serving the pectoral fin rays, consist of the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, arrector dorsalis and coracoradialis. The protractor pectoralis is also described in this section.

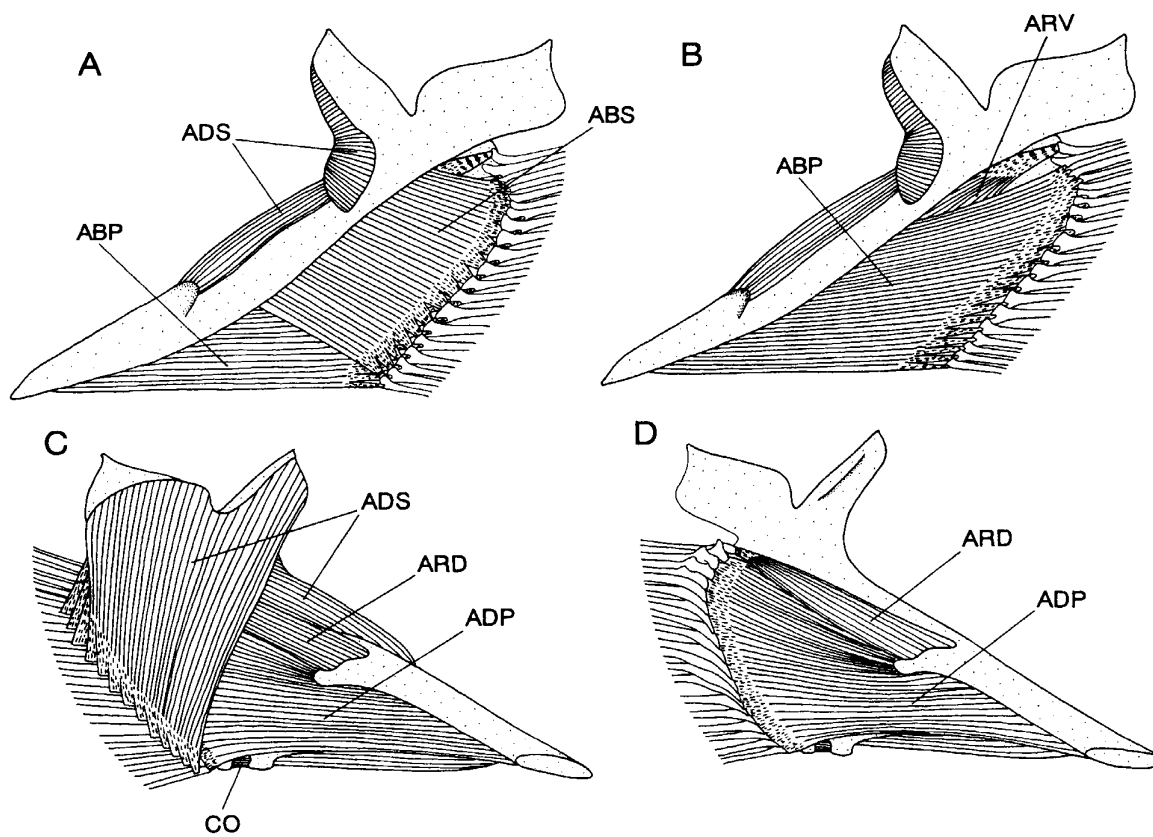


Fig. 44. Lateral (A and B) and medial (C and D) aspects of pectoral girdle in *Thysanophrys chiltonae*. B, after removal of ABS; D, after removal of ADS. Scale indicates 5mm.

The abductor superficialis is a superficial muscle on the lateral surface of the pectoral girdle. It originates from the posterior face of the wing of the cleithrum and is inserted onto the basal portion of each pectoral fin ray, except the uppermost.

The abductor profundus is the medial division of the lateral pectoral muscles. It originates from the medial surface of the cleithrum and the lateral surfaces of the inner actinosts and coracoid, and is inserted onto the basal portion of each ray.

The arrector ventralis is located on the medial aspect of the abductor superficialis and the dorsal aspect of the abductor profundus. It originates mainly from the medial surface of the cleithrum, and is inserted onto the base of the uppermost ray.

The adductor superficialis, a dorsomedial muscle on the medial surface of the pectoral girdle, originates from the anteromedial surface of the cleithrum and is inserted onto the base of each ray, except the uppermost.

The adductor profundus is located on the lateral aspect of the adductor superficialis. It originates broadly from the medial aspect of the pectoral girdle, and is inserted onto each ray, except the uppermost.

The arrector dorsalis is located on the lateral and dorsal aspects of the adductor superficialis and adductor profundus, respectively. It originates from the medial surfaces of the cleithrum and scapula, and is inserted onto the basal portion of the uppermost ray.

The coracoradialis interconnects the posterior border of the coracoid and the

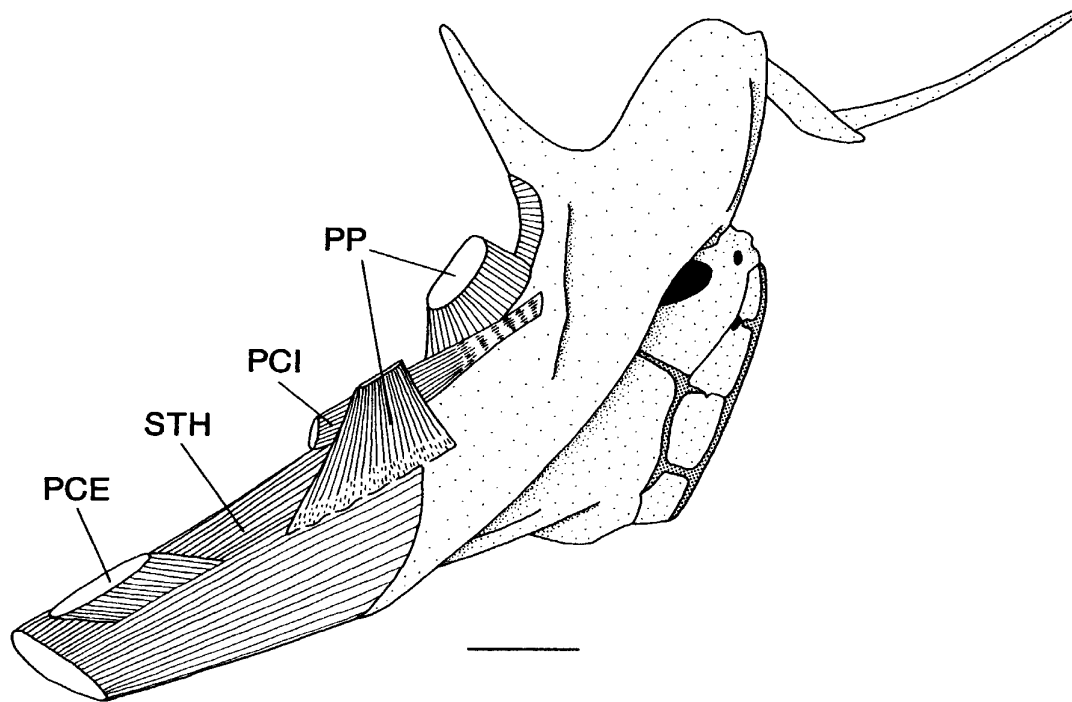


Fig. 45. Lateral aspect of muscles associated with pectoral girdle in *Neoplatycephalus richardsoni*. Scale indicates 5mm.

lowermost actinost.

The protractor pectoralis is divided into two elements, anterior and posterior. The anterior element is sheet-like, the posterior element being more robust. Both originate from the posterolateral corner of the neurocranium, the former being inserted onto the posterior portion of the sternohyoideus and cleithrum via sheet-like connective tissue continuous with the muscle, and the posterior onto the cleithrum directly (Fig. 45).

Characters

No derived characters suitable for analysis were recognized.

Other variations

None.

Pelvic fin muscles (Fig. 46)

Description

The pelvic fin muscles, serving the pelvic fin rays, consist of both dorsal and ventral elements. The dorsal elements include the adductor superficialis pelvis, adductor profundus pelvis, arrector dorsalis pelvis and extensor proprius, and the ventral elements include the abductor superficialis pelvis, abductor profundus pelvis and arrector ventralis pelvis.

The adductor superficialis pelvis overlies the adductor profundus pelvis, and is connected with the outer three soft rays and spine via long, strong tendons (Fig. 46A).

The adductor profundus pelvis originates from the dorsal surface of the pelvis

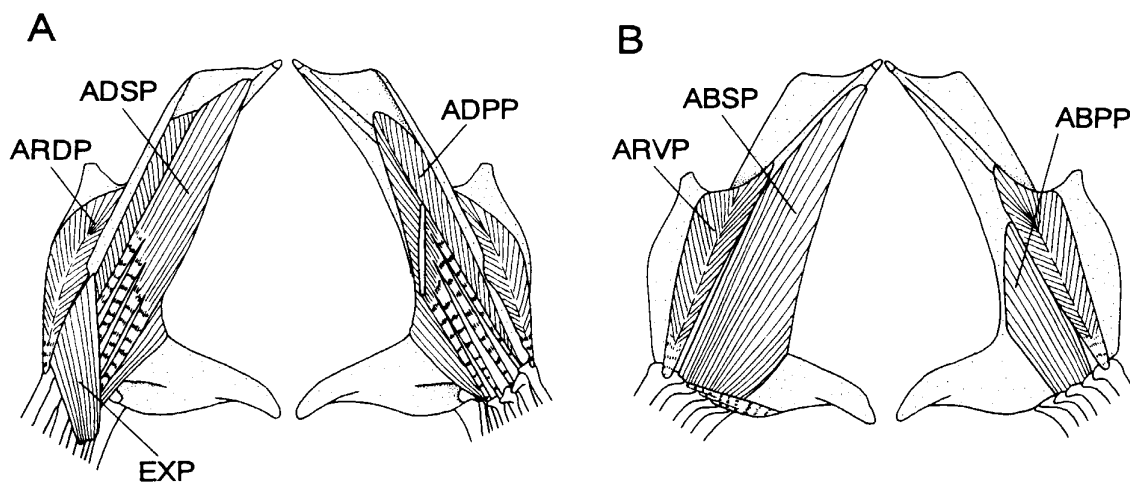


Fig. 46. Dorsal (A) and ventral (B) aspects of pelvic muscles in *Thysanophrys chiltonae*. A, right side, after removal of ADSP; B, right side, after removal of ABSP. Scale indicates 5mm.

and is inserted onto the soft fin ray bases.

The arrector dorsalis pelvici originates from the lateral surface of the pelvis and is inserted onto the base of the spine.

The extensor proprius originates from the dorsolateral border of the pelvis and is inserted onto some of the inner rays.

The abductor superficialis pelvici overlies the abductor profundus pelvici and is connected with all soft ray and spine bases.

The abductor profundus pelvici originates from the ventral surface of the pelvis and is inserted onto the base of the soft rays.

The arrector ventralis pelvici originates from the lateral margin of the ventral surface of the pelvis and is inserted onto the base of the spine.

Characters

No derived characters suitable for analysis were recognized.

Other variations

None.

Caudal fin muscles (Fig. 47)

Description

The caudal fin muscles, serving the caudal fin rays, consist of the interradiialis, hypochordal longitudinalis, flexor dorsalis superior, flexor dorsalis, flexor ventralis, flexor ventralis externus and flexor ventralis inferior. The adductor dorsalis is absent.

The interradiialis, interconnecting the caudal fin rays, splits into dorsal and ventral elements, associated with the dorsal and ventral lobes of the caudal fin, respectively.

The hypochordal longitudinalis is a triangular muscle, originating from the hypurals, parhypural and urostyle, and being inserted onto several upper caudal fin rays via long and strong tendons.

The flexor dorsalis superior originates mainly from the epurals and neural spine(s) and is inserted onto the caudal fin ray bases at the posterodorsal corner of

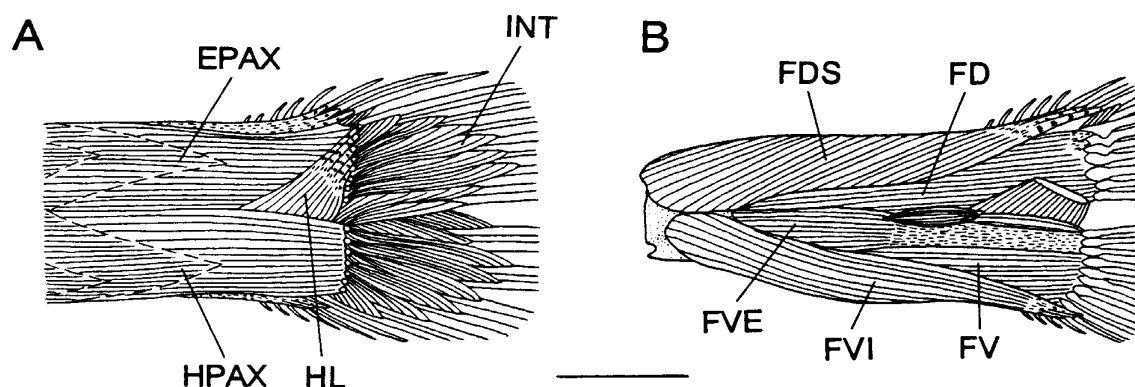


Fig. 47. Lateral aspect of caudal fin muscles in *Suggrundus meerdervoortii*. A, superficial view; B, after removal of EPAX and HPAX. Scale indicates 5mm.

the caudal fin (Fig. 47B).

The flexor dorsalis originates from the epurals, uronural, urostyle and second preural centrum, and is inserted onto the bases of the upper lobe fin rays.

The flexor ventralis originates from the urostyle, lower hypural, parhypural, hemal spine(s) and second preural centrum, and is inserted onto the bases of the lower lobe fin rays.

The flexor ventralis externus originates from the hemal spines and is inserted onto the bases of some upper fin rays of the lower lobe via a long tendon.

The flexor ventralis inferior originates from the hemal spines and second (and third) preural centrum, and is inserted onto the caudal fin rays at the posteroventral corner of the caudal skeleton.

Characters

No derived characters suitable for analysis were recognized.

Other variations

None.

Swimbladder and associated muscles (Fig. 48)

Description

The muscles usually associated with the swimbladder are the extrinsic and intrinsic, the latter being absent in all platycephalids. The obliquus superioris is also described here.

A swimbladder is absent in all platycephalids, except *Neoplatycephalus*, *Suggrundus rodericensis*, *Sorsogona prionota* and *S. nigripinna*.

The extrinsic muscle, a paired muscle, is present in all platycephalids, originating from the posteroventral border of the neurocranium and medial aspect of the supracleithrum, and being inserted, via a membranous tendon, onto the parapophyses of the abdominal vertebrae while running dorsally to the obliquus superioris.

The obliquus superioris, lying below the horizontal septum, extends to the posteroventral surface of the neurocranium. This muscle is penetrated by Baudelot's ligament (Fig. 48B) except in *Platycephalus fuscus*, in which it lies dorsally to the ligament (Fig. 48A).

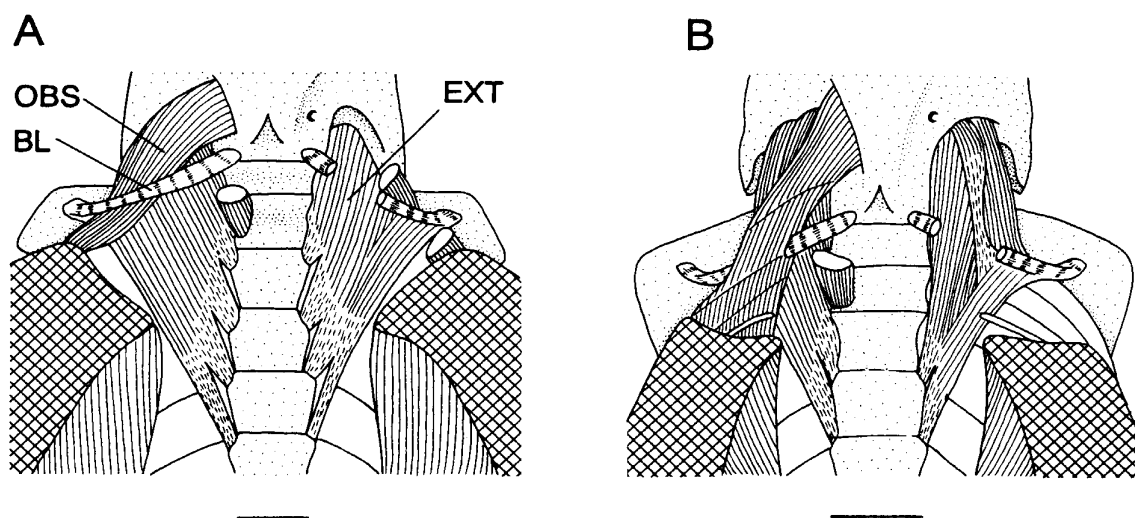


Fig. 48. Ventral aspect of roof of abdominal cavity. A, *Platycephalus fuscus*; B, *Thysanophrys chiltonae*. Scales indicate 5mm.

Characters

TS 96. Swimbladder

0: absent; 1: present. The swimbladder is present in *Neoplatycephalus*, *Suggrundus rodericensis*, *Sorsogona prionota* and *S. nigripinna*.

Outgroups. It is absent in all outgroups, except triglids and peristediids.

Polarity. ON=0 or 1.

Remarks. This character was not used in the first analysis, because both conditions have been recorded for the scorpaenid *Pontinus macrocephalus* (absence [Matsubara 1943] and presence [Ishida 1994; pers. obs.]).

TS 97. Obliquus superioris and Baudelot's ligament

0: penetrated by the ligament; 1: not penetrated. The muscle is not penetrated by the ligament in *Platycephalus fuscus*.

Outgroups. Baudelot's ligament penetrates the obliquus superioris in all outgroups, except the triglid *Pterygotrigla*, peristediids, and the hoplichthyids *Hoplichthys langsdorfii* and *H. haswelli*, in which the muscle is absent.

Polarity. ON=0.

Other variations

None.

III. External morphology (Figs 49-53)

Scales in the lateral line, ocular flap, lip papillae, pit behind the eye and interopercular flap have all been used as important taxonomic characters (Matsubara and Ochiai 1955; Knapp 1973, 1984, 1986; Imamura and Amaoka 1994; Imamura *et al.* 1996). Recently, the sensory tubes on the cheek region were recognized as a valid taxonomic character (Imamura *et al.* 1995; Imamura and Amaoka 1996). These characters are described and discussed in this section.

Description

Scales in the lateral line. Most scales have a downward opening posteriorly in

Platycephalus, *Neoplatycephalus conatus*, *Elates*, *Ratabulus*, *Cociella*, *Suggrundus rodericensis*, *Grammoplites scaber*, *G. suppositus* and *Cymbacephalus* (Fig. 49A, B), but have both downward and upward openings posteriorly in other platycephalids (Fig. 49C-F). All lateral line scales bear a strong, backwardly directed spine in *Grammoplites* (Fig. 49B, C). The lateral line scales also usually have ctenii posteriorly, although such spines are absent in *Grammoplites gruveli* and *Thysanophrys cirronasa* (Fig. 49C).

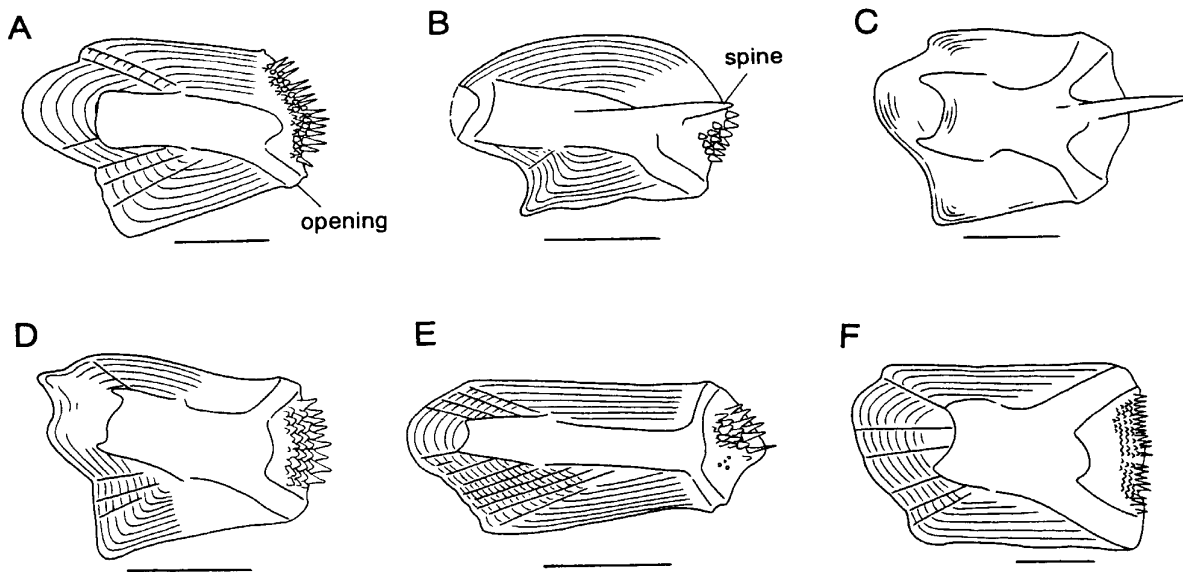


Fig. 49. Lateral aspect of midbody lateral line scales. A, *Suggrundus rodericensis*; B, *Grammoplites scaber*; C, *G. gruveli*; D, *S. macracanthus*; E, *Papilloculiceps longiceps*; F, *Thysanophrys chiltonae*. Scales indicate 1mm.

Ocular flap. A single flap is present in *Papilloculiceps*, *Thysanophrys armata* and *Onigocia* (Fig. 50A), and many flaps in *Cymbacephalus nematophthalmus*, *C. beauforti* and *Thysanophrys cirronasa* (Fig. 50B). A flap is absent in other platycephalids.

Interopercular flap. An interopercular flap, comprising skin only, is present on the lower margin of the gill opening in *Platycephalus caeruleopunctatus*, *P. fuscus*, *Suggrundus*, *Inegocia*, *Papilloculiceps* and *Cymbacephalus* (Fig. 51B), but absent in other platycephalids (Fig. 51A).

Lip papillae. In the platycephalids, only *Grammoplites portuguesus* and *Thysanophrys otaitensis* bear the papillae on the lips (Fig. 52).

Pit behind eye. A pit behind the eye is present in all *Cymbacephalus* (Fig. 50B), but absent in other platycephalids (Fig. 50A).

Sensory tubes on cheek region. Thin sensory tubes from the first and second infraorbitals and the preopercle extend to the cheek region in many platycephalids. In *Platycephalus marmoratus*, *Cymbacephalus nematophthalmus*, *Suggrundus macracanthus*, *Thysanophrys otaitensis* and *T. arenicola*, they are weakly developed, extending to, but not completely covering, the cheek region (Fig. 53B). The tubes are well-developed, extending to and completely covering the cheek region in *Grammoplites gruveli*, *G. portuguesus*, *Suggrundus meerdervoortii*, *S. cooperi*, *Onigocia*,

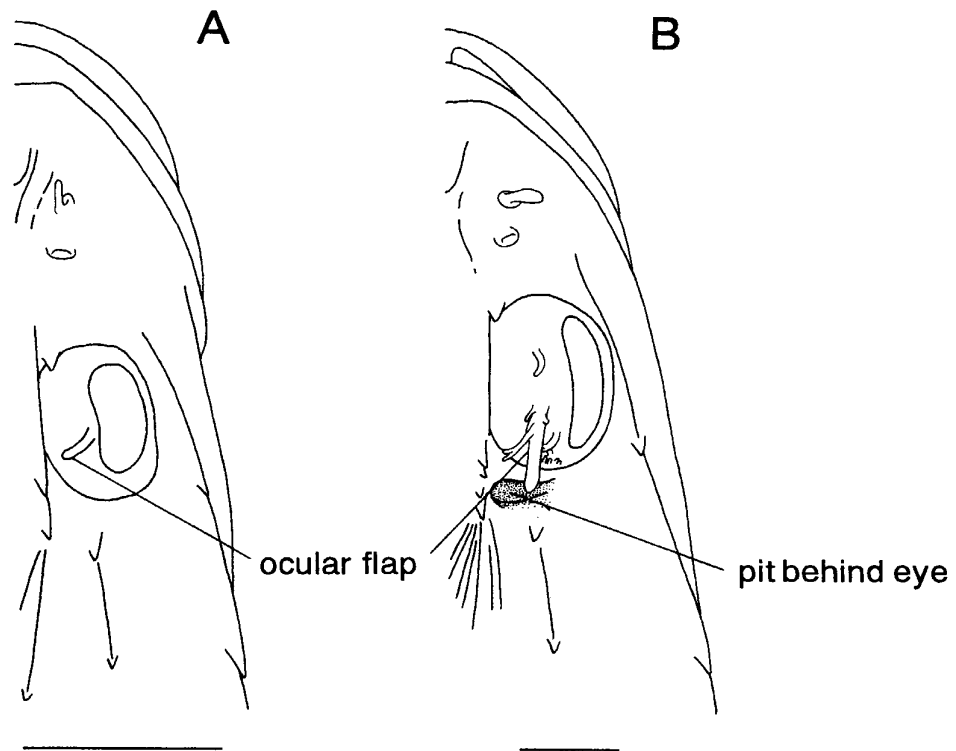


Fig. 50. Dorsal aspect of head region. A, *Papilloculiceps longiceps*; B, *Cymbacephalus nematophthalmus*. Scales indicate 5mm.

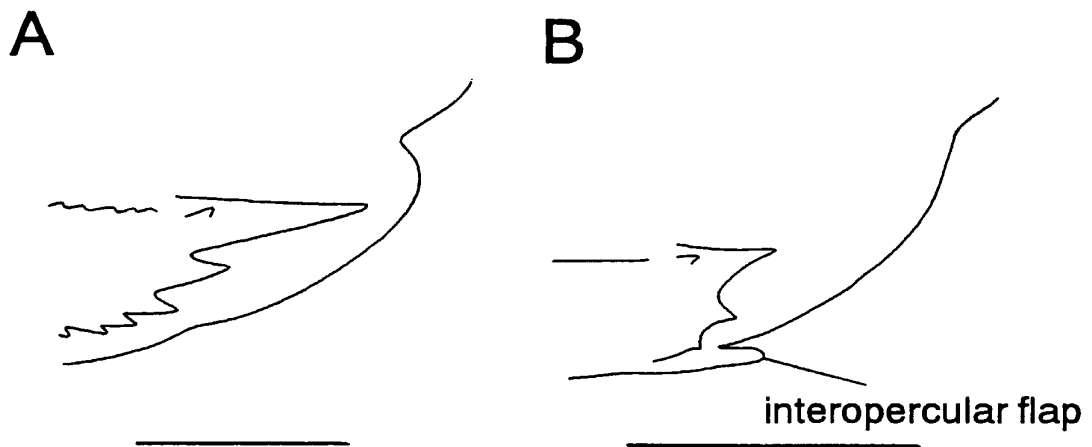


Fig. 51. Lateral aspect of opercular region. A, *Sorsogona tuberculata*; B, *Inegocia japonica*. Scales indicate 5mm.

Rogadius, *Sorsogona* and *Thysanophrys*, except *T. otaitensis* and *T. arenicola* (Fig. 53C). In other platycephalids, they are not developed and do not extend to the cheek region (Fig. 53A).

Characters

TS 98. Number of openings to exterior on lateral line scales

0: one; 1: two. One opening is found in *Platycephalus*, *Neoplatycephalus conatus*, *Elates*, *Ratabulus*, *Cociella*, *Suggrundus rodericensis*, *Grammoplites scaber*, *G. suppositus*

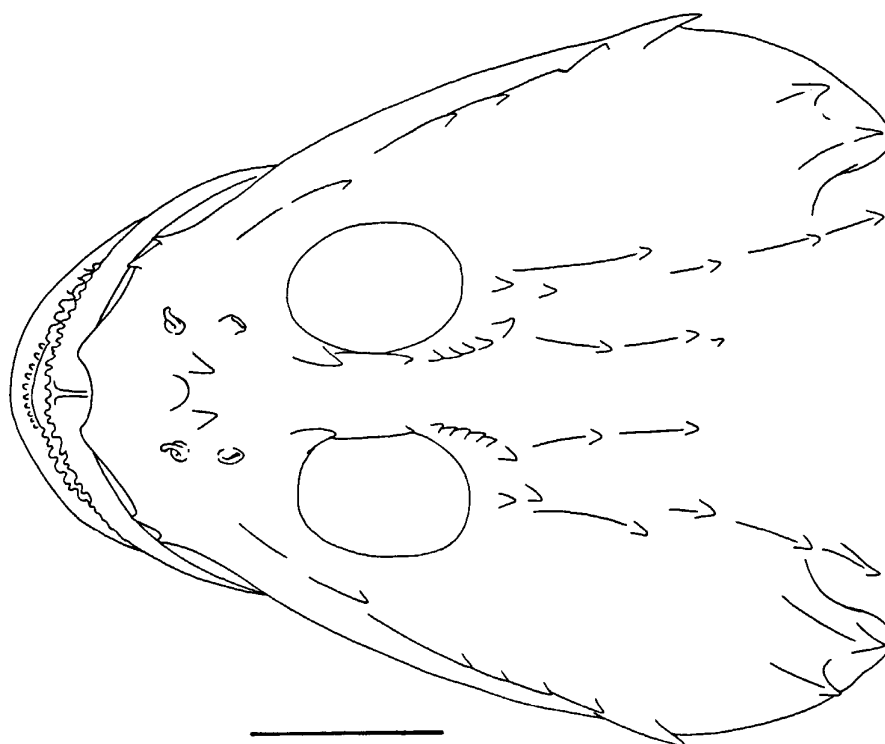


Fig. 52. Dorsal aspect of head region of *Thsanophrys otaitensis* (from Imamura *et al.* 1995). Scale indicates 10mm.

and *Cymbacephalus*, and two openings in other platycephalids.

Outgroups. All outgroups, except *Chelidonichthys* and *Lepidotrigla*, which have more than two openings, have a single opening.

Polarity. ON = 0.

TS 99. Distinct spine on scales in lateral line

0: several anteriormost scales with a spine; 1: all scales with a spine. All lateral line scales have a spine in *Grammolites*.

Outgroups. A few anterior scales in the lateral line have a spine in all outgroups, except peristediids and hoplichthyids, which have one or two distinct spines on each scale.

Polarity. ON = 0.

TS 100. Lateral line scales

0: with ctenii posteriorly; 1: without ctenii. Lateral line scales lack ctenii in *Grammolites gruvelli* and *Thysanophrys cirronasa*.

Outgroups. Lateral line scales have ctenii in all outgroups, except peristediids and hoplichthyids. In the latter, ctenii are absent owing to the scales being highly modified.

Polarity. ON = 0.

TS 101. Ocular flap

0: absent; 1: single flap present; 2: many flaps present. A single flap is present in *Papilloculiceps longiceps*, *Thysanophrys armata* and *Onigocia*, and many in

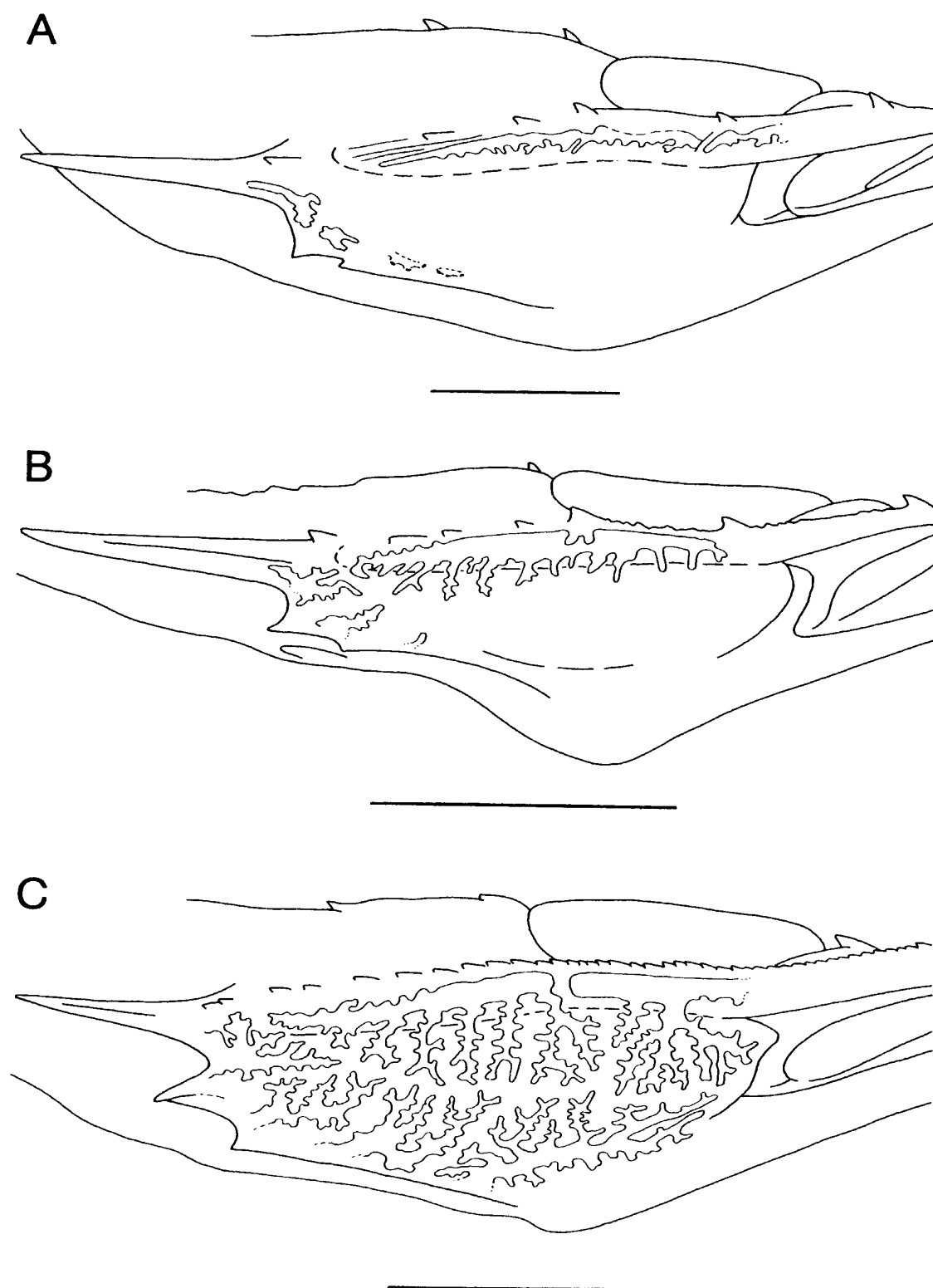


Fig. 53. Ventrolateral aspect of head region. A, *Grammoplites suppositus*; B, *Suggrundus macracanthus*; C, *Sorsogona prionota*. Scales indicate 10mm.

Cymbacephalus nematophthalmus, *C. beauforti* and *Thysanophrys cirronasa*.

Outgroups. All outgroups lack ocular flaps.

Polarity. ON=0 (ordered as 0-1-2).

TS 102. Interopercular flap

0: absent; 1: present. An interopercular flap is found in *Platycephalus caeruleopunctatus*, *P. fuscus*, *Suggrundus*, *Inegocia*, *Papilloculiceps* and *Cymbacephalus*.

Outgroups. The flap is absent in all outgroups.

Polarity. ON=0.

Remarks. Ochiai (1984) and Shao and Chen (1987) mentioned that *Thysanophrys chiltonae* has an "interopercular flap." However, such is not homologous to the flap seen in other species, because it is supported by the interopercle. The flap in other species comprises unsupported skin only.

TS 103. Lip papillae

0: absent; 1: present. Papillae are found in *Grammoplites portuguesus* and *Thysanophrys otaitensis*.

Outgroups. All outgroups lack lip papillae.

Polarity. ON=0.

TS 104. Pit behind eye

0: absent; 1: present. A pit is present in *Cymbacephalus*.

Outgroups. A pit is absent in all outgroups.

Polarity. ON=0.

TS 105. Sensory tubes on cheek region

0: not developed; 1: weakly developed; 2: well developed. Weakly developed tubes are found in *Platycephalus marmoratus*, *Cymbacephalus nematophthalmus*, *Suggrundus macracanthus*, *Thysanophrys arenicola* and *T. otaitensis*. The tubes are well developed in *Suggrundus*, except *S. rodericensis* and *S. macracanthus*, *Thysanophrys cirronasa*, *T. chiltonae*, *T. armata*, *Onigocia*, *Sorsogona*, *Rogadius*, *Grammoplites gruveli* and *G. portuguesus*.

Outgroups. *Prionotus* has weakly developed sensory tubes on the cheek region, whereas other outgroups lack them.

Polarity. ON=0 (ordered as 0-1-2).

Other variations

Size of interopercular flap. The interopercular flap is very large in *Cymbacephalus*, but small in *Platycephalus caeruleopunctatus*, *P. fuscus*, *Suggrundus*, except *S. rodericensis*, *Inegocia* and *Papilloculiceps*. However, size was not used in the analysis, since intraspecific variation is found at least in *S. rodericensis*.

Configuration of ocular flap. In *Thysanophrys cirronasa*, intraspecific variation is found in the configuration of the ocular flap (entirely cylindrical or posteriorly fan-like). Therefore, configuration could not be used in the analysis.

Configuration of iris lappet. Configuration of the iris lappet has been considered as an important taxonomic character in platycephalids (Knapp 1973, 1979, 1984, 1991, 1996; Imamura and Amaoka 1994; Imamura *et al.* 1995, 1996). However, it was not used in the analysis, because of intraspecific variations in configuration in *Grammoplites suppositus*, *Suggrundus rodericensis* and *S. macracanthus*.

Table 1. Matrix of characters in 32 transformation series for examined platycephalids. "?" indicates that the outgroup node is unspecified.

SPECIES	TRANSFORMATION SERIES						
	74-75	76-80	81-85	86-90	91-95	96-100	101-105
1. OUTGROUP NODE	00	??00?	00000	0000?	00000	?0000	00000
2. <i>Neoplatycephalus conatus</i>	01	01001	10011	10000	21002	10000	00000
3. <i>N. richardsoni</i>	01	01001	00011	10000	21002	10100	00000
4. <i>Platycephalus fuscus</i>	01	01011	10001	10000	11002	01000	01000
5. <i>P. caeruleopunctatus</i>	01	01011	10001	10000	21001	00000	01000
6. <i>P. marmoratus</i>	01	01011	10000	00000	21001	00000	00001
7. <i>P. bassensis</i>	01	01011	00000	00000	21001	00000	00000
8. <i>P. longispinis</i>	01	01001	00000	00000	21001	00000	00000
9. <i>Elates ransonneti</i>	00	01101	00100	00000	21011	00000	00000
10. <i>Ratabulus megacephalus</i>	00	01100	01000	00010	00100	00000	00000
11. <i>R. diversidens</i>	00	01100	01000	00010	00100	00000	00000
12. <i>Cociella crocodila</i>	00	01100	00000	00011	00000	00000	00000
13. <i>Grammoplites scaber</i>	00	01100	00000	00011	00000	00010	00000
14. <i>G. suppositus</i>	00	11100	00000	00011	00000	00010	00000
15. <i>G. gruveli</i>	00	01100	00000	00011	00000	00111	00002
16. <i>G. portuguesus</i>	10	12100	00000	00011	00000	00110	00102
17. <i>Cymbacephalus beauforti</i>	00	01100	00000	00011	00000	00000	21010
18. <i>C. nematophthalmus</i>	00	01100	00000	00011	00000	00000	21011
19. <i>C. staigeri</i>	00	01100	00000	00011	00000	00000	01010
20. <i>Papilloculiceps longiceps</i>	00	01100	00000	00011	00000	00100	11000
21. <i>Inegocia japonica</i>	00	01100	00000	00011	00000	00100	01000
22. <i>Suggrundus meerdervoortii</i>	00	11100	00000	00011	00000	00100	01002
23. <i>S. cooperi</i>	00	11100	00000	00011	00000	00100	01002
24. <i>S. macracanthus</i>	00	11100	00000	00011	00000	00100	01001
25. <i>S. rodericensis</i>	00	11100	00000	00011	00000	10000	01000
26. <i>S. jugosus</i>	10	01100	00000	00011	00000	00100	01002
27. <i>Thysanophrys arenicola</i>	00	01100	00000	00211	00000	00100	00001
28. <i>T. armata</i>	00	01101	00000	00011	00000	00100	10002
29. <i>T. chiltonae</i>	00	01101	00000	00111	00000	00100	00002
30. <i>T. cirronasa</i>	01	01101	00000	00010	00000	00101	20002
31. <i>T. otaitensis</i>	00	01100	00000	00211	00000	00100	00101
32. <i>Onigocia macrolepis</i>	10	01100	00000	00011	00000	00100	10002
33. <i>O. spinosa</i>	10	02100	00000	00011	00000	00100	10002
34. <i>Rogadius asper</i>	10	11100	00000	01011	00000	00100	00002
35. <i>R. pristiger</i>	10	11100	00000	01011	00000	00100	00002
36. <i>R. patriciae</i>	10	11100	00000	00011	00000	00100	00002
37. <i>Sorsogona tuberculata</i>	10	12100	00000	00011	00000	00100	00002
38. <i>S. nigripinna</i>	10	12100	00000	00011	00000	10100	00002
39. <i>S. prionota</i>	10	12100	00000	00011	00000	10100	00002

Phylogenetic relationships within Platycephalidae

Apomorphic characters in 32 transformation series were accepted for the second-step analysis of the relationships within the Platycephalidae (Table 1). "0" represents plesiomorphic and "1" and "2" apomorphic characters, except in TS 76, 77, 80, 90 and 96, in which the outgroup node is not specified. The interrelationships of 38 platycephalid species were reconstructed on the basis of 2 equally parsimonious trees, which were seen in a terminal clade, L1 (Figs 54, 56). The consistency index was 0.561 and the tree length 66.

The relationships within Platycephalidae are shown in Figures 54-56. Monophyly of this taxon is supported by apomorphies 16-1, 23-1, 42-2, 54-1, 58-1 and 61-1. Clade E2 is divided into clades H1 and H2.

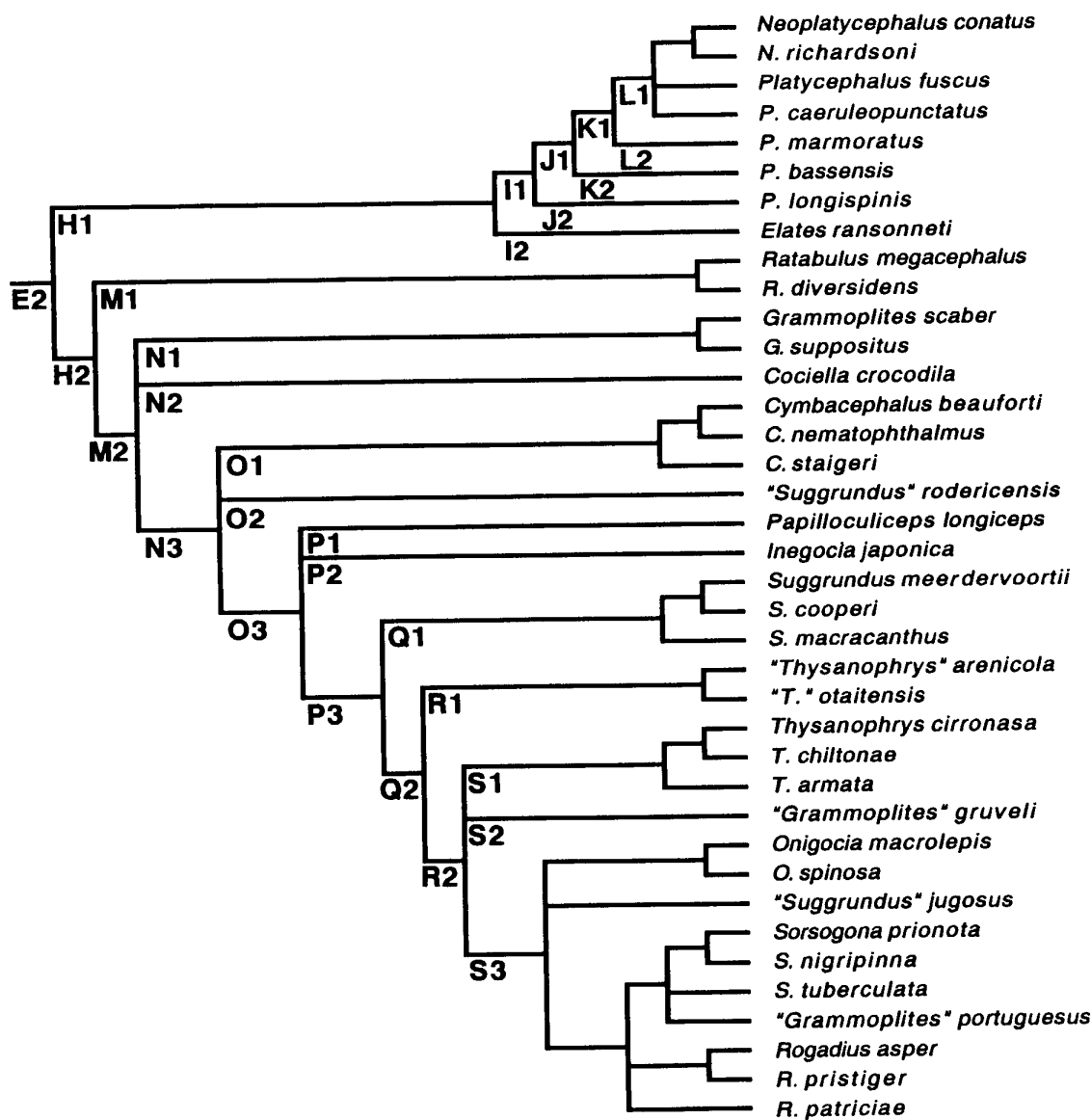


Fig. 54. Strict consensus tree of 2 equally parsimonious cladograms of 38 platycephalid species.

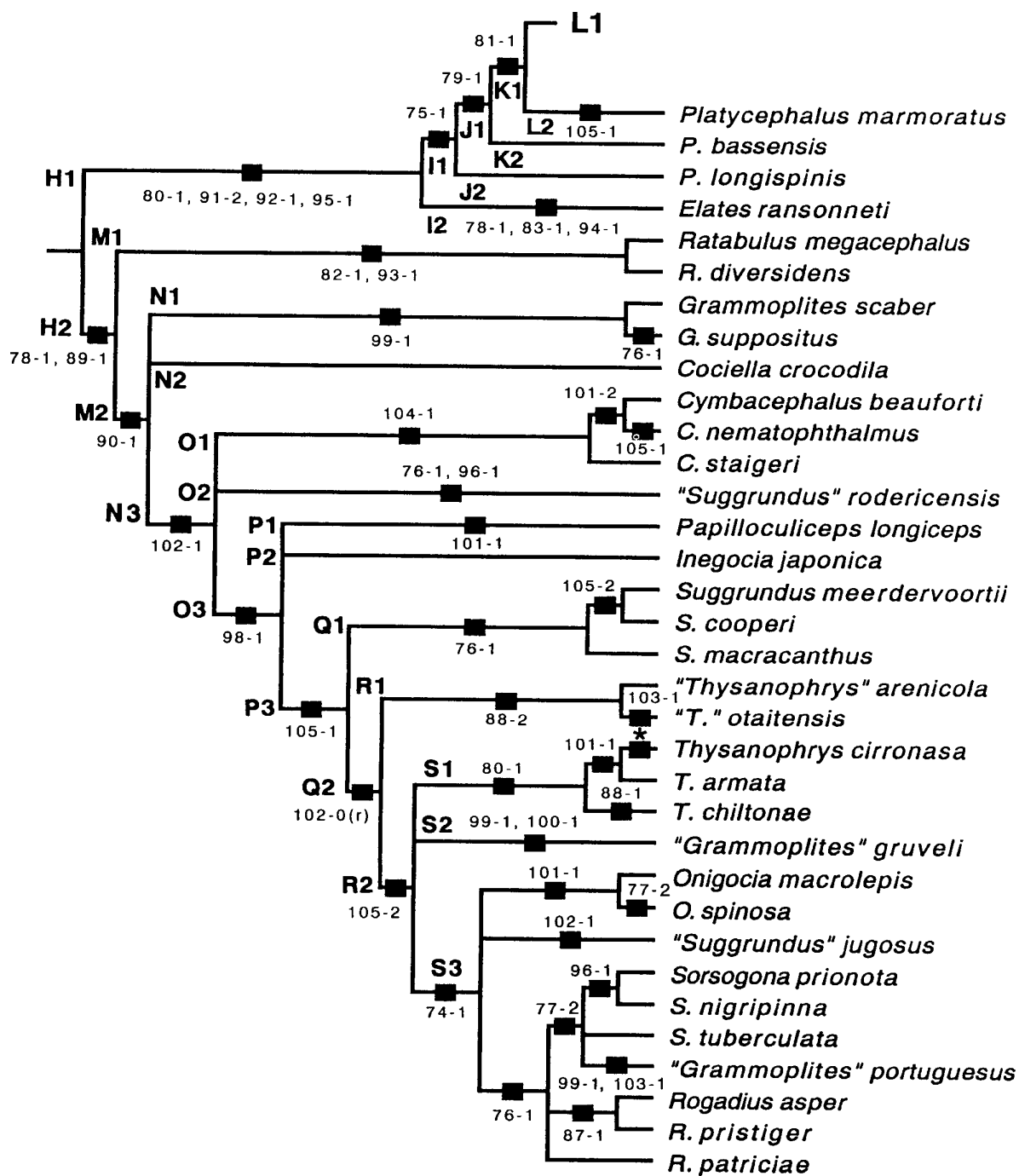


Fig. 55. Cladogram and character distributions in Platycephalidae. Numbers of transformation series correspond to those of Table 1.

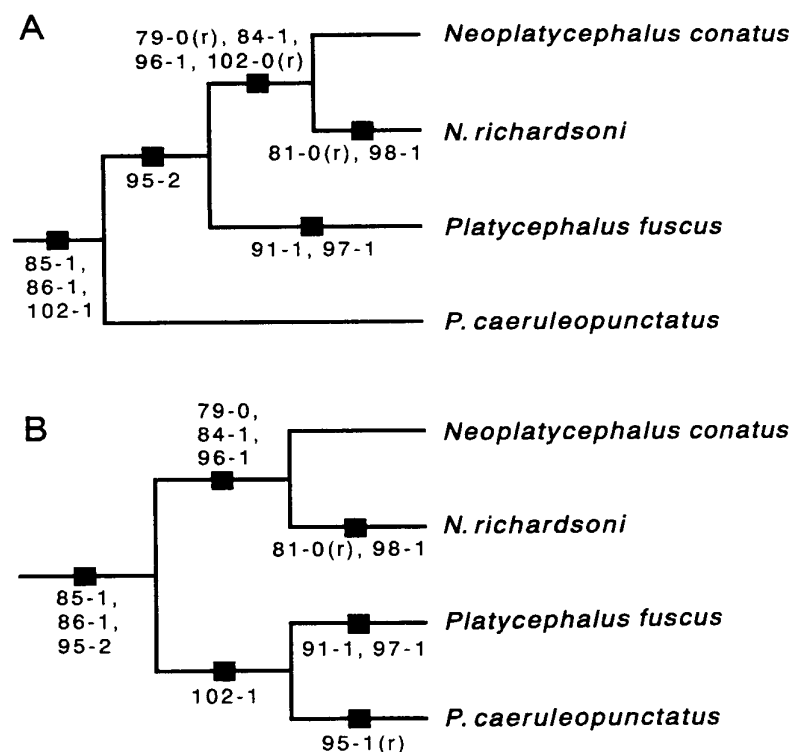


Fig. 56. Two equally parsimonious cladograms in clade L1, including two species of *Neoplatycephalus*, *Platycephalus fuscus* and *P. caeruleopunctatus*. Numbers of transformation series correspond to those of Table 1.

Clade H1. Includes *Platycephalus*, *Neoplatycephalus* and *Elates*, being supported by apomorphies 80-1, 91-2, 92-1 and 95-1. This clade is divided into clades I1 and I2.

Clade I1. Includes all *Platycephalus* and *Neoplatycephalus*, which are supported by a single derived character 75-1. Clade I1 is divided into clades J1 and J2.

Clade J1. Includes *Neoplatycephalus* and *Platycephalus*, except *P. longispinis*, and is characterized by 79-1. Clade J1 is divided into clades K1 and K2.

Clade J2. Includes only *P. longispinis*, which has no derived characters.

Clade K1. Includes *Neoplatycephalus* and *Platycephalus*, except *P. longispinis* and *P. bassensis*, being supported by a single apomorphy 81-1. It is divided into clades L1 and L2.

Clade K2. Only *P. bassensis*, which has no defining apomorphies, is included.

Clade L1. Includes *Neoplatycephalus*, *P. fuscus* and *P. caeruleopunctatus*, characterized by 85-1 and 86-1. Two hypotheses exist regarding the relationships of these species: (1) *Neoplatycephalus* and *P. fuscus* represent a monophyletic group, with *P. caeruleopunctatus* a sister group (Fig. 56A), or (2) *P. caeruleopunctatus* and *P. fuscus* represent a monophyletic group, with *Neoplatycephalus* a sister group (Fig. 56B). In the former hypothesis, *Neoplatycephalus*, *P. fuscus* and *P. caeruleopunctatus* share apomorphy 102-1, with *Neoplatycephalus* and *P. fuscus* also sharing apomorphy 95-2. In the latter hypothesis, *Neoplatycephalus*, *P. fuscus* and *P. caeruleopunctatus* all share apomorphy 95-2, *P. fuscus* and *P. caeruleopunctatus* share apomorphy 102-1, and *P. caeruleopunctatus* undergoes a character reversal 95-1[r]. *Platycephalus fuscus* is characterized by 91-1 and 97-1, and *Neoplatycephalus* by 79-0[r], 84-1 and 96-1. In the

former hypothesis, *Neoplatycephalus* is also characterized by 102-0[r], with *N. conatus* having no further apomorphies, and *N. richardsoni* having 81-0[r] and 98-1.

The two hypotheses have equal possibility at this stage.

Clade L2. Includes only *P. marmoratus*, characterized by a single apomorphy 105-1.

Clade I2. *Elates ransonneti* is the only species included, being characterized by 78-1, 83-1 and 94-1.

Clade H2. Includes all platycephalid genera, except *Platycephalus*, *Neoplatycephalus* and *Elates*, being supported by apomorphies 78-1 and 89-1. This clade is divided into clades M1 and M2.

Clade M1. Includes only *Ratabulus*, supported by apomorphies 82-1 and 93-1. Neither *R. megacephalus* nor *R. diversidens* have any additional derived characters.

Clade M2. Includes all platycephalid genera, except *Neoplatycephalus*, *Platycephalus*, *Elates* and *Ratabulus*, being supported by a single apomorphy 90-1. It branches into clades N1 to N3.

Clade N1. Includes *Grammoplites scaber* and *G. suppositus*, which share apomorphy 99-1. Although *G. scaber* lacks additional derived characters, *G. suppositus* has a further apomorphy 76-1.

Clade N2. Includes only *Cociella crocodila*, which has no derived characters.

Clade N3. Includes *Cymbacephalus*, "*Suggrundus*" *rodericensis*, *Inegocia*, *Papilloculiceps*, *Thysanophrys*, *Onigocia*, *Rogadius*, *Sorsogona*, *Suggrundus*, "*Grammoplites*" *gruveli* and "*G.*" *portuguesus*, supported by apomorphy 102-1. Clade N3 is divided into three clades, O1, O2 and O3, with unclear relationships.

Clade O1. Includes all *Cymbacephalus*, characterized by 104-1. *Cymbacephalus nematophthalmus* and *C. beauforti* share apomorphy 101-2, *C. nematophthalmus* additionally having apomorphy 105-1. *Cymbacephalus staigeri* and *C. beauforti* lack additional derived characters.

Clade O2. Includes only "*Suggrundus*" *rodericensis*, characterized by two apomorphies, 76-1 and 96-1.

Clade O3. Includes *Inegocia*, *Papilloculiceps*, *Thysanophrys*, *Onigocia*, *Rogadius*, *Sorsogona*, *Suggrundus*, "*Grammoplites*" *gruveli* and "*G.*" *portuguesus*, being supported by apomorphy 98-1. This clade is divided into three clades, P1, P2 and P3, with unresolved relationships.

Clade P1. Includes only *Papilloculiceps*, with a single apomorphy 101-1.

Clade P2. Includes only *Inegocia*, which has no derived characters.

Clade P3. Includes *Thysanophrys*, *Onigocia*, *Rogadius*, *Sorsogona*, *Suggrundus*, "*Grammoplites*" *gruveli* and "*G.*" *portuguesus*, sharing a single apomorphy 105-1. It is divided into clades Q1 and Q2.

Clade Q1. Includes *Suggrundus meerdervoortii*, *S. macracanthus* and *S. cooperi*, sharing a single apomorphy 76-1. *S. meerdervoortii* and *S. cooperi* are supported by apomorphy 105-2. Neither species has any further apomorphic characters.

Clade Q2. Includes *Thysanophrys*, *Onigocia*, "*Suggrundus*" *jugosus*, *Rogadius*, *Sorsogona*, "*Grammoplites*" *gruveli* and "*G.*" *portuguesus*, with a single apomorphy 102-0[r]. Q2 is divided into clades R1 and R2.

Clade R1. Includes "*Thysanophrys*" *arenicola* and "*T.*" *otaitensis*, being supported by apomorphy 88-2. Additional derived characters are absent in "*T.*" *arenicola*, but "*T.*" *otaitensis* has one, 103-1.

Clade R2. Includes *Thysanophrys*, except "*T.*" *arenicola* and "*T.*" *otaitensis*,

Onigocia, "*Suggrundus*" *jugosus*, *Rogadius*, *Sorsogona*, "*Grammoplites*" *gruveli* and "*G.*" *portuguesus*, being supported by apomorphy 105-2. This clade is divided into clades S1, S2 and S3, with uncertain relationships.

Clade S1. Includes *Thysanophrys cirronasa*, *T. chiltonae* and *T. armata*, which share character 80-1. *Thysanophrys cirronasa* and *T. armata* are further characterized by 101-1, and *T. cirronasa* by 75-1, 90-0[r], 100-1 and 101-2. *Thysanophrys armata* lacks any additional apomorphic characters, but *T. chiltonae* has one, 88-1.

Clade S2. Includes only "*Grammoplites*" *gruveli*, with apomorphies 99-1 and 100-1.

Clade S3. Includes *Onigocia*, "*Suggrundus*" *jugosus*, *Sorsogona*, "*Grammoplites*" *portuguesus* and *Rogadius*, supported by apomorphy 74-1.

Onigocia comprises a monophyletic group, which is supported by apomorphy 101-1; while *O. macrolepis* lacks any derived characters, *O. spinosa* has one, 77-2.

"*Suggrundus*" *jugosus* has a single apomorphy 102-1.

Rogadius, *Sorsogona* and "*Grammoplites*" *portuguesus* share a single derived character 76-1, *Sorsogona* and "*G.*" *portuguesus* additionally having apomorphy 77-2, *S. prionota* and *S. nigripinna* apomorphy 96-1, and "*G.*" *portuguesus* apomorphies 99-1 and 103-1. *Sorsogona tuberculata* lacks additional characters. *Rogadius asper* and *R. pristiger* share apomorphy 87-1, but no additional derived characters were found in *R. patriciae*.

Comparison with previous works

Relationships of Platycephalidae and related taxa. Matsubara and Ochiai (1955) inferred the relationships of Platycephalidae and related taxa using precladistic methodology. They proposed that *Plectrogenium* was initially separated from the other members of the Platycephaloidei, *Parabembras* was separated from a monophyletic group comprising *Bembras*, Hoplichthyidae and Platycephalidae, *Bembras* had a sister relationship with a group including Hoplichthyidae and Platycephalidae, and these last two families were also sister groups. The relationships reconstructed in this study resemble theirs, but differ as follows: *Plectrogenium* is related to *Bembradium*, and Hoplichthyidae comprises a monophyletic group with Triglidae and Peristediidae, together being the sister group of Platycephalidae. *Bembradium*, Triglidae and Peristediidae were not examined by Matsubara and Ochiai (1955).

Washington *et al.* (1984) considered that the scorpaenoid Apistinae might be the primitive sister group of the triglids and peristediids because of several shared characters, including the intrinsic muscle and free pectoral fin rays. However, the peristediids and the triglid *Pterygotrigla* lack intrinsic muscles and the hoplichthyids also have free pectoral fin rays. According to the analysis in this study, the triglids and peristediids share no synapomorphies with *Apistus*, being instead related to the hoplichthyids. On the other hand, *Apistus* is related to *Neosebastes*, *Hypodytes*, *Inimicus*, *Minous* and *Erisphex*, this group being supported by a single synapomorphy (46-1).

Winterbottom (1993) pointed out the resemblance between gobioids and hoplichthyids on the basis of the following 12 apomorphic characters: (1) subquadrangular saccular otolith, (2) otolith with a colliculum that does not reach either margin of the sacculus, (3) posteriorly displaced interhyal, (4) deeply notched

cleithrum, (5) small scapula and coracoid with close association of the middle two radials to the cleithrum, (6) well-developed ventral intercleithral cartilage, (7) articular process for the basipterygia, (8) a broad, domed pelvic girdle, each half being connected anteriorly by a continuous plug of the pelvic intercleithral cartilage, (9) cartilaginous pelvic radial, (10) absence of predorsal, (11) absence of basisphenoid and (12) single dorsal postcleithrum. Of these, the otolith characters (1) and (2) were not examined in this study, and (10) and (12) are not acceptable because of the intraspecific variation found in some platycephaloids. According to the analysis in this study, the hoplichthyids share 8 synapomorphies with the peristediids and 15 with the triglids. Furthermore, 4 synapomorphies link these three taxa and Platycephalidae. In addition, the hoplichthyids share 2 synapomorphies, the backwardly directed opercular spine and an extrinsic muscle derived from the obliquus superioris, with the scorpaenoids and platycephaloids (Scorpaeniformes). Accordingly, it is reasonable to consider that the similar conditions in the gobioids and hoplichthyids are examples of parallelism. Thus, Winterbottom's (1993) hypothesis is not acceptable.

Ishida (1994) included *Plectrogenium*, *Sebastes*, *Sebastiscus*, *Adelosebastes*, *Hozukius*, *Trachyscorpia*, *Helicolenus* and *Sebastolobus* in his Sebastidae on the basis of two synapomorphies, more than 24 vertebrae and elongated tendon of A1, and he considered *Plectrogenium* to be related to *Trachyscorpia*. Ishida's character polarities were determined by using generalized percoids as the outgroup. Matsubara (1943) described intraspecific variations in vertebral numbers in the scorpaenoids, including 24-27 in *Apistus carinatus* and *Hypodytes rubripinnis*, and 23-25 in *Scorpaena izensis*. Furthermore, it is known that the vertebral number in fishes is often variable within a species and may change during early development due to temperature influences. Accordingly, it is inadvisable to use a single defining number (24) for vertebrae. The length of the tendon of A1 was not acceptable for the analysis in this study, because the tendon is "long" or "short" in different percoids (Johnson 1980; Johnson and Freitzsche 1989; pers. obs.) and polarity is uncertain. In this study, the triglids, peristediids and *Plectrogenium* are much more closely related to other platycephaloids by an autapomorphy, presence of a posterior pelvic fossa (36-1), which was described as a noteworthy character in *Plectrogenium* by Matsubara (1943). However, Ishida (1994) neither described nor used this character in his analysis. On the other hand, *Trachyscorpia* is considered to be related to the scorpaenoids in clade A7 on the basis of two synapomorphies, (2-1) and (6-1). Ishida (1994) did not notice the former character in this genus, and did not use the latter in his analysis. Accordingly, I cannot agree with Ishida's (1994) relationships and classification.

Although some authors considered Platycephalidae to include *Parabembras*, *Bembras* and *Bembradium* (Nelson 1984; Shao and Chen 1987; Nakabo 1993), this has been rejected already in this study, because such a grouping is paraphyletic. In addition, *Bembradium* has often been considered to be a member of Bembridae or Platycephalidae (Matsubara 1955; Greenwood *et al.* 1966; Nelson 1984, 1994; Ochiai 1984; Nakabo 1993). However, this genus is linked to *Plectrogenium* by 3 synapomorphies, making inclusion in either Bembridae or Platycephalidae inappropriate.

Parabembridae, established on the basis of *Parabembras* by Jordan and Hubbs (1925), was also recognized by Matsubara (1955). However, subsequently *Para-*

bembras has been included in the family Bembridae (Knapp 1986; Nelson 1994) or in Bembrinae in Platycephalidae (Nelson 1984; Shao and Chen 1987). The latter treatment is not acceptable because *Parabembras* and *Bembras* are not included in the same clade.

Greenwood *et al.* (1966) and Nelson (1976) recognized the suborder Platycephaloidei, and also Hoplichthyoidei for a single family, Hoplichthyidae. Such a treatment is unacceptable because the members of clade A9, aside from Hoplichthyidae, would thereby become a paraphyletic group if these suborders are recognized.

Some authors have included the subfamilies Triglinae and Peristediinae in the family Triglidae, placing the latter in the suborder Scorpaenoidei (Greenwood *et al.* 1966; Nelson 1976, 1984, 1994). However, their Triglidae is not acceptable, because it is a paraphyletic group.

Interrelationships in Platycephalidae. Matsubara and Ochiai (1955) and Keenan (1991) proposed phylogenetic relationships of the family Platycephalidae, based on specimens collected only from local areas: viz. Japanese and Australian waters, respectively. Matsubara and Ochiai's (1955) hypothesis is unacceptable because it was constructed using more subjective, precladistic methodology. Keenan (1991) reconstructed relationships using allozyme electrophoresis, with results resembling those of this study, except in the following: *Neoplatycephalus* was proposed as having a sister relationship with a group including *Platycephalus bassensis* and *P. longispinis*, and *Ratabulus diversidens* and *Suggrundus rodericensis* were thought to comprise a monophyletic group, having a sister relationship with a group containing *Onigocia* and *Sorsogona*. However, such relationships are not acceptable here, owing to the lack of supporting synapomorphies.

Many authors have variously classified the platycephalids into subfamilies and genera. Jordan and Hubbs (1925) recognized 4 subfamilies, Onigociinae, Rogadiinae, Inegociinae and Platycephalinae. Their Inegociinae is paraphyletic and therefore unacceptable, because it contains *Inegocia*, *Insidiator* (= *Suggrundus*), *Cocius* (= *Cociella*) and *Ratabulus*. Although Matsubara and Ochiai (1955) recognized 4 subfamilies, Onigociinae, Inegociinae, Elatinae and Platycephalinae, the members of their Inegociinae followed Jordan and Hubbs (1925). Keenan (1991) separated the Australian platycephalids into 5 subfamilies: Cymbacephalinae, Onigociinae, Inegociinae, Elatinae and Platycephalinae. However, his Inegociinae, including *Inegocia*, *Suggrundus* and *Ratabulus*, is also paraphyletic, and similarly unacceptable.

Although some authors regarded *Neoplatycephalus* as a valid genus or subgenus of *Platycephalus* (Waite 1921; McCulloch 1927; Whitley 1931a; Knapp 1987; Keenan 1991), Paxton *et al.* (1989) considered it to be a junior synonym of *Platycephalus*. In this study, although *Neoplatycephalus* is regarded as monophyletic, the former *Platycephalus* constitutes a paraphyletic group. Accordingly, *Neoplatycephalus* is not recognized, in accordance with cladistic theory.

Keenan (1991) revived the genus *Longitrudis* Whitley, 1931, which had been rarely used following its proposal (Whitley 1931b), including in it *Platycephalus bassensis* and *P. longispinis*. This genus is, however, unacceptable because it is now seen to be paraphyletic.

Fowler (1904) defined *Grammoplites* for species having a distinct spine on all of the lateral line scales. Although Imamura and Amaoka (1994) recognized five species in the genus (*G. scaber*, *G. suppositus*, *G. portuguesus*, *G. gruvelli* and *G. knappi*

Imamura and Amaoka, 1994), the present study shows the group to be polyphyletic.

Platycephalus rodericensis Cuvier, 1829 has been considered a member of the genus *Suggrundus* (Knapp 1984, 1992; Gloerfelt-Tarp and Kailola 1984; Shao and Chen 1987; Paxton *et al.* 1989), and *Insidiator jugosus* McCulloch, 1914 was also included in *Suggrundus* by Paxton *et al.* (1989). However, these species do not comprise a monophyletic group with *S. meerdervoortii*, the type species of the genus, and the above treatments cannot therefore be supported.

Although *Thysanophrys* Ogilby, 1898, including seven species, has been regarded as a valid group (Knapp 1984, 1986; Shao and Chen 1987; Paxton *et al.* 1989; Imamura *et al.* 1995), it is in fact paraphyletic.

Although *Rogadius* was defined by Jordan and Richardson (1908) as a group having an antrorse preopercular spine, such is absent in *R. patriciae*, recently described by Knapp (1987). The analysis disclosed no synapomorphies supporting *Rogadius* (*sensu* Knapp 1987), and his grouping is therefore not accepted.

Classification

Suborder **Platycephaloidei**

Diagnosis. Posterior pelvic fossa present (Fig. 5); first dorsal proximal pterygiophore inserted into space between second and third neural spines; second and third dorsal proximal pterygiophores inserted into space between third and fourth neural spines (except in peristediid *Peristedion*) (Fig. 57A).

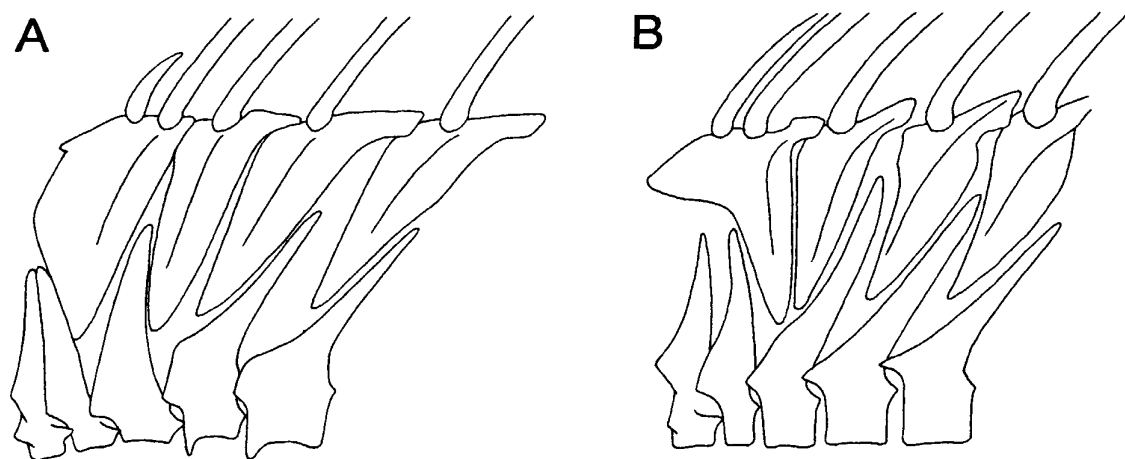


Fig. 57. Diagrammatic illustration of anterior vertebrae and associated bones. A, *Plectrogenium nanum* (Platycephaloidei); B, *Sebastiscus marmoratus* (Scorpaenoidei).

Families in suborder Platycephaloidei. Seven families are recognized for the suborder Platycephaloidei, on the basis of their phylogenetic relationships (Fig. 58).

- Family Plectrogeniidae
- Family Parabembridae
- Family Bembridae

Family Triglidae
 Family Peristediidae
 Family Hoplichthyidae
 Family Platycephalidae

Remarks. The suborder Platycephaloidei differs from Scorpaenoidei in having a posterior pelvic fossa (absent in Scorpaenoidei), and the first, and second and third dorsal proximal pterygiophores inserted into the spaces between the second and third, and third and fourth neural spines, respectively (Fig. 57A). An exception is the the peristediid *Peristedion*, in which the first and second pterygiophores are inserted into the space between the second and third neural spines, with the third pterygiophore inserted between the third and fourth spines, as in many scorpaenoids (Fig. 57B). However, the polarity of the characters in the latter transformation series is uncertain, because both conditions are common in percoids (Johnson 1984).

On the basis of clade E2 comprising the family Platycephalidae, family rank was ascribed to six other clades (B1, C1, D1, F1, G1 and G2) for the suborder (Fig. 58). All of these families were already established previous authors, and no additional new families are necessary for this ranking. Although it is also cladistically resonable to provide family rank for clade E1 and subfamily rank for claders F1 , G1 and G2, a subfamily Hoplichthyinae has not previously been proposed.

Although *Plectrogenium*, Triglidae and Peristediidae have not previously been regarded as members of the Platycephaloidei (Matsubara 1943, 1955; Greenwood *et al.* 1966; Nelson 1994; etc.), the suborder (*sensu* Nelson 1984), as recognized up to now, has been paraphyletic. The present grouping of families resolved this.

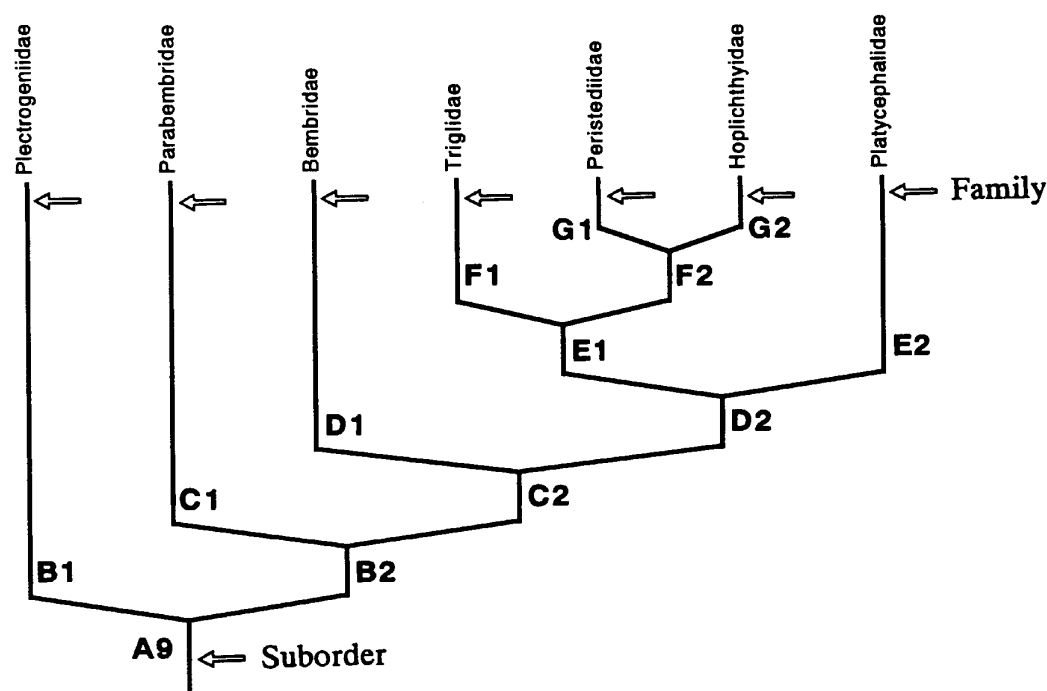


Fig. 58. Phylogenetic relationships within Platycephaloidei and family-level ranking. Numbers of clades correspond to those in Figures 2, 3 and 4.

Key to the families of Platycephaloidei

- 1a. Scales in lateral line modified as bony plates2
- 1b. Scales in lateral line not modified3
- 2a. Body covered by bony platesPeristediidae
- 2b. Body completely or mostly nakedHoplichthyidae
- 3a. Lower jaw projecting beyond the upper jaw when mouth closed4
- 3b. Lower jaw shorter than or level with upper jaw when mouth closed5
- 4a. Anal fin with spinesParabembridae
- 4b. Anal fin lacking spinesPlatycephalidae
- 5a. Pectoral fin with 3 free raysTriglidae
- 5b. Pectoral fin lacking free rays6
- 6a. More than 40 lateral line scalesBembridae
- 6b. Less than 30 lateral line scalesPlectrogeniidae

Family Plectrogeniidae

Diagnosis. Dorsal surface of head with spines, but lacking tubercles; sensory canal between pterotic and preopercle absent; stay cartilaginous; pectoral fin lacking free rays; transversus dorsalis anterior not branched (Fig. 6B); lateral line scales less than 30; swimbladder absent.

Remarks. This family includes two genera, *Plectrogenium* and *Bembradium*, both having been formerly included in different families. *Plectrogenium* was regarded as a member of the scorpaenid subfamily Plectrogeninae (misspelled, should be spelled Plectrogeniinae) (Matsubara 1943, 1955; Nelson 1994) or Sebastidae (Ishida 1994), whereas *Bembradium* was included in Platycephalidae (Greenwood *et al.* 1966; Ochiai 1984; Nelson 1984; Nakabo 1993) or Bembridae (Nelson 1994). Such treatments are untenable, since the genera comprise a monophyletic group, supported by a platycephaloid character (presence of a posterior pelvic fossa).

Family Parabembridae

Diagnosis. Dorsal surface of head with spines only; lower jaw projecting beyond upper jaw when mouth closed; ascending process and remaining part of premaxillary separated; pectoral fin lacking free rays; anal fin with three spines; lateral line scales about 35-40; swimbladder absent.

Remarks. This family contains a single genus, *Parabembras*. Although Jordan and Hubbs (1925) established Parabembridae, many subsequent authors have placed the genus in the family Bembridae (Knapp 1986; Nelson 1994) or subfamily Bembrinae (Platycephalidae) (Nelson 1984; Shao and Chen 1987), Matsubara (1955) following Jordan and Hubbs (1925). Parabembridae is recognized here, since *Parabembras* is not included in clade D1 (with *Bembras*, type genus of its own family).

Family **Bembridae**

Diagnosis. Dorsal surface of head with spines only; lower jaw slightly shorter than upper jaw when mouth closed; pectoral fin lacking free rays; anal fin lacking spines; lateral line scales about 50; swimbladder absent.

Remarks. Although some authors included *Bembradium* and *Parabembras* in the family Bembridae (Knapp 1986; Nelson 1994), such a grouping, being paraphyletic, is unacceptable.

The family includes a single genus, *Bembras*.

Family **Triglidae**

Diagnosis. Dorsal surface of head with spines and tubercles (Fig. 9B); lachrymal and second infraorbital meeting; second and fourth infraorbitals meeting; pectoral fin with 3 free rays; flexor ventralis externus absent; intrinsic muscle usually present (absent in *Pterygotrigla*); swimbladder present.

Remarks. This family has previously been included in the suborder Scorpaenoidei (Greenwood *et al.* 1966; Nelson 1984, 1994). However, Triglidae should be transferred to the suborder Platycephaloidei, owing to triglids sharing a synapomorphy (posterior pelvic fossa present) with other platycephaloids.

The family includes about 10 genera according to Nelson (1994).

Family **Peristediidae**

Diagnosis. Dorsal surface of head with spines and tubercles (Fig. 9C); nasals on both sides sutured medially (Fig. 9C); tooth plates on the prevomer absent; cartilaginous basihyal (Fig. 11C); tooth plate on second and third epibranchials absent (Fig. 7F); pectoral fin with 2 free rays; bony plates present on body; swimbladder present.

Remarks. Some authors have treated the present family as the subfamily Peristediinae of Triglidae (Greenwood *et al.* 1966; Nelson 1984, 1994). However, such a ranking is unacceptable, because it is paraphyletic if Hoplichthyidae is excluded. The present treatment is in keeping with that of Matsubara (1955).

The family includes four genera, *Gargariscus*, *Heminodus*, *Peristedion* and *Satyrichthys* (Nelson 1994).

Family **Hoplichthyidae**

Diagnosis. Dorsal surface of head with spines and tubercles (Fig. 9A); fifth infraorbital fused with sphenotic (Fig. 9A); sensory canal between neurocranium and preopercle absent; ascending process and remaining part of the premaxillary separated; metapterygoid lamina and entopterygoid absent (Fig. 10B); hypohyals and basihyal articulated (Fig. 11B); first pharyngobranchial cartilaginous (Fig. 7D); tooth plate on second pharyngobranchial absent (Fig. 7D); anal fin lacking spines; pectoral fin with free rays; levator posterior absent (Fig. 6C); lateral line scales modified as bony plates; body scales mostly or completely absent; swimbladder

absent.

Remarks. Greenwood *et al.* (1966) and Nelson (1976) recognized the suborder Hoplichthyoidei, including only the family Hoplichthyidae. However, recognition of a separate suborder would thus render the Platycephaloidei paraphyletic. Accordingly, Hoplichthyidae is regarded as a member of Platycephaloidei.

The family includes a single genus, *Hoplichthys* (Nelson 1994).

Family **Platycephalidae**

Diagnosis. Lower jaw projecting beyond upper jaw when mouth closed; ascending process and remaining part of premaxillary separated (Fig. 21); urohyal sutured with first basibranchial (Fig. 27); posteromedial parts of pelvic bones separated (Fig. 32); second spine on first anal proximal pterygiophore absent (Fig. 37C); sternohyoideus originating from lateral and ventral aspects of urohyal (Fig. 42B); protractor pectoralis consisting of sheet-like anterior and robust posterior elements (Fig. 45); adductor superficialis pelvici connected to rays via a long and strong tendon (Fig. 46); pectoral fin usually rounded posteriorly (concave in *Kumococius rodericensis*) and lacking free rays; anal fin lacking spines.

Subfamilies and genera in the family Platycephalidae. Two subfamilies and 17 genera, including 3 newly established, are recognized in Platycephalidae (Fig. 59).

Subfamily Platycephalinae

Genus *Platycephalus* Bloch, 1795

Genus *Elates* Jordan and Seale, 1905

Subfamily Onigociinae

Genus *Ratabulus* Jordan and Hubbs, 1925

Genus *Grammoplites* Fowler, 1904

Genus *Cociella* Whitley, 1940

Genus *Cymbacephalus* Fowler, 1938

Genus *Kumococius* Matsubara and Ochiai, 1955

Genus *Papilloculiceps* Fowler and Steinitz, 1956

Genus *Inegocia* Jordan and Richardson, 1908

Genus *Suggrundus* Whitley, 1930

Genus *Eurycephalus* gen. nov.

Genus *Thysanophrys* Ogilby, 1898

Genus *Solitas* gen. nov.

Genus *Onigocia* Jordan and Thompson, 1913

Genus *Ambiserrula* gen. nov.

Genus *Rogadius* Jordan and Richardson, 1908

Incertae sedis: genus *Leviprora* Whitley, 1931

Remarks. Two subfamilies, for clades H1 (Platycephalinae) and H2 (Onigociinae) (Fig. 59) are recognized in this study. Although some authors have recognized other subfamilies; viz. Cymbacephalinae, Elatinae, Grammoplitinae, Inegociinae, Rogadiinae and Thysanophryinae (Jordan and Hubbs 1925; Whitley 1931a; Fowler 1938; Matsubara and Ochiai 1955; Keenan 1991), these names are not retained here because the members of clades H1 and H2 are poorly defined by few or

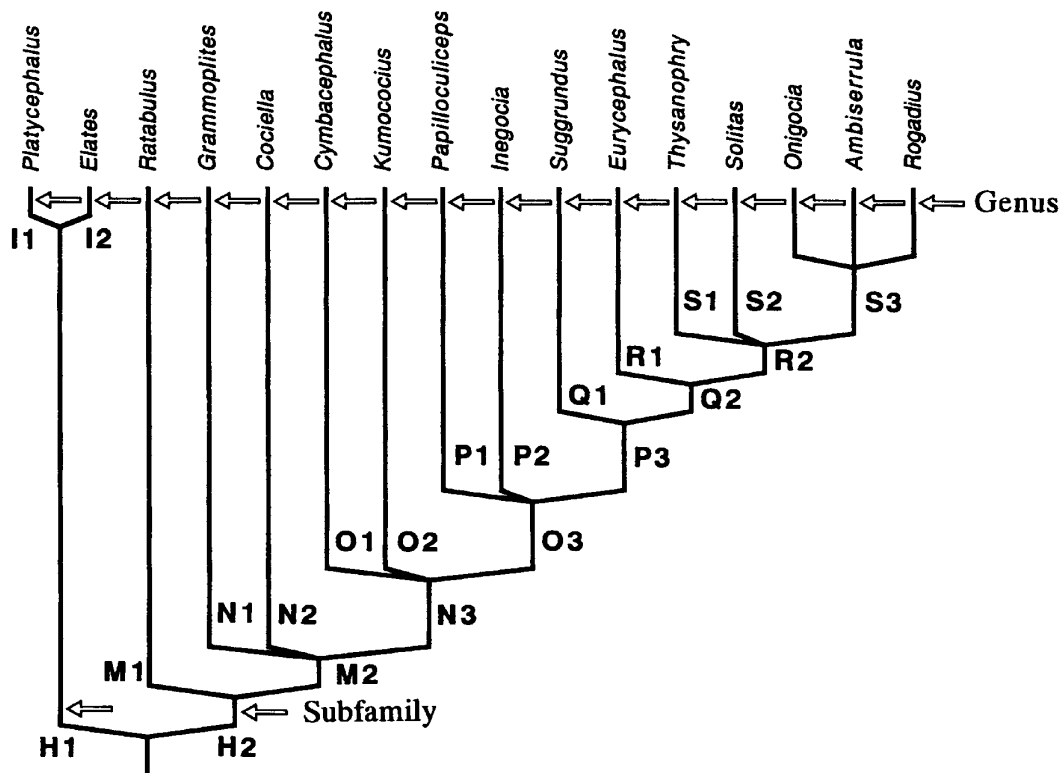


Fig. 59. Phylogenetic relationships within Platycephalidae and ranking at subfamily and generic levels. Numbers of clades correspond to those in Figures 54 and 55.

no derived characters. (The subfamily Onigocinae was established with Inegocinae and Rogadiinae by Jordan and Hubbs [1925]. The former is selected here as the subfamily name for clade H2, according to ICZN [1985] Recomm. 24A. Moreover, Cymbacephalinae, Grammoplitinae and Thysanophryinae were established later.)

Sixteen genera are recognized, most having been previously regarded as valid taxa (Fig. 59). *Leviprora* is retained, since the internal characters of the only known species, *L. inops*, could not be examined in this study and its phylogenetic position is uncertain. New definitions and discussions of the subfamilies and genera are included under "Remarks" for each taxon. Both internal characters and external characters are included in the subfamilial and generic diagnoses.

Key to the subfamilies of Platycephalidae

- 1a. Lateral line scales usually more than 60, urohyal and second basibranchial separatedPlatycephalinae
- 1b. Lateral line less scales than 60, urohyal and second basibranchial suturedOnigocinae

Subfamily **Platycephalinae**

Diagnosis. Dorsal surface of head with spines only (Fig. 13); urohyal separated from second basibranchial (Fig. 27A, B); interarcual cartilage present (Fig. 30A); spine on second dorsal proximal pterygiophore very short (Fig. 34C, D); adductor arcus palatini or levator arcus palatini extending to frontal (Figs 38, 39); preopercle usually with one (*Elates*), or two (rarely three) spines (*Platycephalus*) posteriorly; lateral line scales usually more than 60 (59-65 in *Platycephalus chauliodous* according to Knapp 1991); ocular flaps absent.

Remarks. As presently recognized, the subfamily includes two genera, *Platycephalus* and *Elates*.

Key to the genera of Platycephalinae

- 1a. Prevomer with a single tooth plate, preopercle with two (rarely three) spines *Platycephalus*
 1b. Prevomer with two tooth plates, preopercle with one spine *Elates*

Genus ***Platycephalus*** Bloch, 1795

Platycephalus Bloch, 1795: 96 (type species: *P. spathula* Bloch, 1795 [junior synonym of *Callionymus indicus* Linnaeus, 1758]).

Calliomorus Lacépède, 1800: 343 (type species: *Callionymus indicus*)

Neoplatycephalus Castelnau, 1872: 87 (type species: *P. grandis* Castelnau, 1872 [junior synonym of *P. richardsoni* Castelnau, 1872]).

Cacumen Whitley, 1931b: 326 (type species: *P. speculator* Klunzinger, 1872).

Planiprora Whitley, 1931b: 327 (type species: *P. fuscus* Cuvier, 1829).

Trudis Whitley, 1931b: 327 (type species: *P. bassensis* Cuvier, 1829).

Longitrudis Whitley, 1931b: 327 (type species: *P. longispinis* Macleay, 1884).

Colefaxia Whitley, 1935: 249 (type species: *Platycephalus macrodon* Ogilby, 1885 [junior synonym of *P. richardsoni*]).

Diagnosis. Suborbital lacking prominent spines (Fig. 12A); prevomer with one tooth plate (Fig. 13); preopercle with two spines (rarely three) (Fig. 23A); lateral line scales usually with one opening to exterior (two in *P. richardsoni*); sensory tubes on cheek region absent or weakly developed.

Remarks. *Neoplatycephalus* was established by Castelnau (1872), being characterized by very large, stout canines on the palatine. Although some authors recognized it as a valid genus or subgenus (Waite 1921; McCulloch 1927; Knapp 1987; Keenan 1991), Paxton *et al.* (1989) did not. Although *Neoplatycephalus* was recognized as a monophyletic group in this study, *Platycephalus* becomes paraphyletic if the former is given a similar (generic or subgeneric) rank. Accordingly, generic rank is given to *Platycephalus*, it being the monophyletic group included in clade II. *Neoplatycephalus* thus becomes a junior synonym of *Platycephalus*.

Whitley (1931b) established 4 new genera (*Cacumen*, *Planiprora*, *Trudis* and *Longitrudis*) for the members of *Platycephalus* defined here. They were poorly

defined, the few differing external characters being better regarded as having species-level significance only, when compared with other species of *Platycephalidae*. Moreover, *Platycephalus* monophyly would not be maintained if *Planiprora* and *Trudis* were recognized. Although Keenan (1991) revived *Longitrudis* for *P. bassensis* and *P. longispinis*, it would be a paraphyletic group according to this study. Accordingly, all 4 of Whitley's genera are regarded as junior synonyms of *Platycephalus*.

Platycephalus includes at least the following species: *P. arenaris* Ramsey and Ogilby, 1886, *P. aurimaculatus* Knapp, 1987, *P. bassensis* Cuvier, 1829, *P. caeruleopunctatus* McCulloch, 1922, *P. cultellatus* Richardson, 1846, *P. chauliodous* Knapp, 1991, *P. conatus* Waite and McCulloch, 1915, *P. endrachtensis* Quay and Gaimard, 1825, *P. fuscus* Cuvier, 1829, *P. indicus* (Linnaeus, 1758) (= type species) (Fig. 60), *P. laevigatus* Cuvier, 1829, *P. longispinis* Cuvier, 1829, *P. marmoratus* Stead, 1908, *P. richardsoni* Castelnau, 1872 and *P. speculator* Klunzinger, 1872.

Although Japanese specimens of *Platycephalus* had been identified as a single species (*P. indicus*) by many authors (Matsubara and Ochiai 1955; Matsubara 1955; Knapp 1984, 1986; Ochiai 1984; etc.), they in fact represent *P. indicus* and two undescribed species (Sakashita 1992).

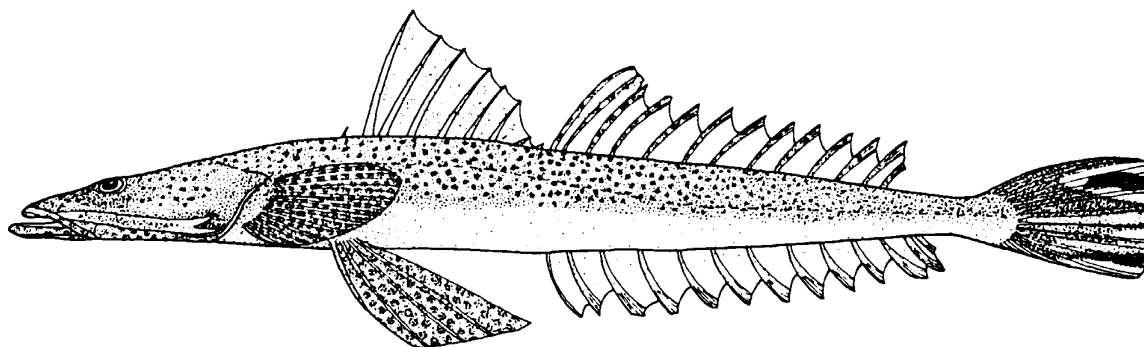


Fig. 60. Lateral aspect of *Platycephalus indicus*, type species of the genus (from Knapp 1984).

Material examined. *Platycephalus bassensis*: AMS I.12796 (172mm), Tasmania, Australia (43°02'S, 147°22'E), date unknown.

P. conatus: FSFL EB494 (247mm), Western Australia (30°20.9'S, 115°02.5'E), 241 m, 16 Nov. 1975.

P. longispinis: AMS I.24802-001 (178mm), Australia (35°04'S, 150°41'E), 8 m, 17 March 1984.

Genus *Elates* Jordan and Seale, 1907

Elates Jordan and Seale, 1907: 39 (type species: *E. thompsoni* Jordan and Seale, 1907 [junior synonym of *Platycephalus ransonneti* Steindachner, 1877]).

Hyalorhyncus Ogilby, 1910: 118 (type species: *H. pellucidus* Ogilby, 1910 [junior synonym of *P. ransonneti*]).

Diagnosis. Head and body very slender; two suborbital spines present below middle and posterior region of eye; prevomer with two tooth plates; preopercle with

one long spine; lateral line scales with one exterior opening posteriorly; interopercular flap absent; sensory tubes on cheek region not developed.

Remarks. The genus is monotypic, containing only *Elates ransonneti* (Steindachner, 1877) (Fig. 61).

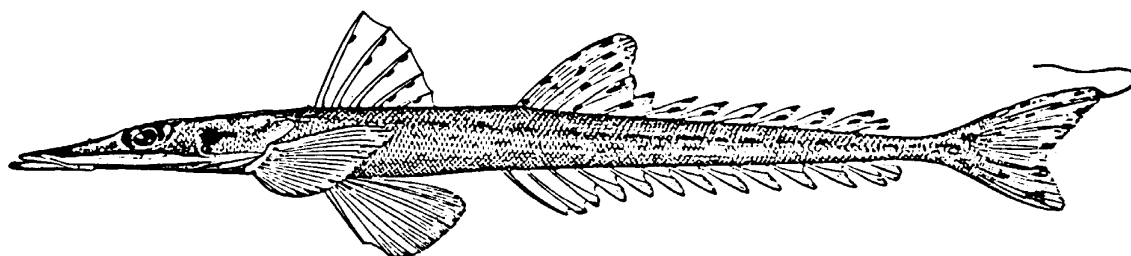


Fig. 61. Lateral aspect of *Elates ransonneti*, type species of the genus (from Jordan and Seale 1907).

Material examined. *Elates ransonneti*: FUMT-P 8389 (122mm), off Bang Phe, Gulf of Thailand, 40 m, 24 Feb. 1985; FUMT-P 8398 (121mm), off Surat, Gulf of Thailand, 18 Feb. 1985; FUMT-P 8489 (122mm), off Songkhla, Gulf of Thailand, 26-28 m, 27 Feb. 1985; FUMT-P 8944 (110mm), fish market, Songkhla, Thailand, 26 Nov. 1985; HUMZ 109564-109565 (2, 156-166mm), off Sarawak, Borneo Island, South China Sea, 1-8 Dec. 1970.

Subfamily Onigociinae

Diagnosis. Prevomer with two tooth plates (Figs 14-17); preopercle usually with three or more spines (sometimes lowermost indistinct) (Fig. 23B-F); urohyal sutured with second basibranchial (Fig. 27B, D); interarcual cartilage present (*Ratabulus* and *Thysanophrys cirronasa*) or absent (others) (Fig. 30B-D); spine on second dorsal proximal pterygiophore long (Fig. 34B); no muscles extending to frontal (Fig. 36); lateral line scales less than 60.

Remarks. At present, the subfamily comprises 15 genera, including 3 new genera, *Ambiserrula*, *Eurycephalus* and *Solitas*.

Key to the genera of Onigociinae

- 1a. Jaws, palatine and pharyngobranchials with villiform or small canine teeth ...2
- 1b. Jaws, palatine and pharyngobranchials with long, slender canine teeth
.....*Ratabulus*.....3
- 2a. Pit behind eye absent3
- 2b. Pit behind eye present*Cymbacephalus*.....4
- 3a. Sensory tubes on cheek region not developed4
- 3b. Sensory tubes on cheek region weakly or well-developed9
- 4a. Ocular flap present*Papilloculiceps*.....5
- 4b. Ocular flap absent.....5
- 5a. All lateral line scales with a distinct spine.....*Grammoplites*

- 5b. Several anterior lateral line scales with a distinct spine6
- 6a. Suborbital ridge without spines*Leviprora*
- 6b. Suborbital ridge with spines7
- 7a. Pectoral fin concave posteriorly*Kumococius*
- 7b. Pectoral fin rounded posteriorly8
- 8a. Preorbital spine absent*Inegocia*
- 8b. Preorbital spine present*Cociella*
- 9a. Interopercular flap present10
- 9b. Interopercular flap absent11
- 10a. Iris lappet bilobed or scalloped*Suggrundus*
- 10b. Iris lappet long and branched*Ambiserrula* gen. nov.
- 11a. Tubercles on head present*Rogadius*
- 11b. Tubercles on head absent12
- 12a. All lateral line scales with a distinct spine.....*Solitas* gen. nov.
- 12b. Several anterior scales in lateral line with a distinct spine.....13
- 13a. Cheek region incompletely covered by weakly developed sensory tubes
.....*Eurycephalus* gen. nov.
- 13b. Cheek region completely covered by well developed sensory tubes14
- 14a. More than 45 lateral line scales*Thysanophrys*
- 14b. Less than 45 lateral line scales.....*Onigocia*

Genus *Ratabulus* Jordan and Hubbs, 1925

Ratabulus Jordan and Hubbs, 1925: 286 (type species: *Thysanophrys megacephalus* Tanaka, 1917).

Diagnosis. Dorsal surface of head with spines only (Fig. 14); suborbital ridge usually with four or more distinct spines; jaws, palatine, prevomer and pharyngobranchials with very long, slender canine teeth (Figs 14, 22A, 23B, 30B); lateral line scales with one exterior opening posteriorly; iris lappet absent; ocular and interopercular flaps absent; sensory tubes on cheek region not developed.

Remarks. *Ratabulus* contains two species, *R. diversidens* (McCulloch, 1914) and *R. megacephalus* (Tanaka, 1917) (= type species) (Fig. 62).

A free spine between the dorsal fins is a useful character for distinguishing the two species of this genus from other platycephalids, although *Grammoplites knappi* rarely has the spine (Imamura and Amaoka 1994).

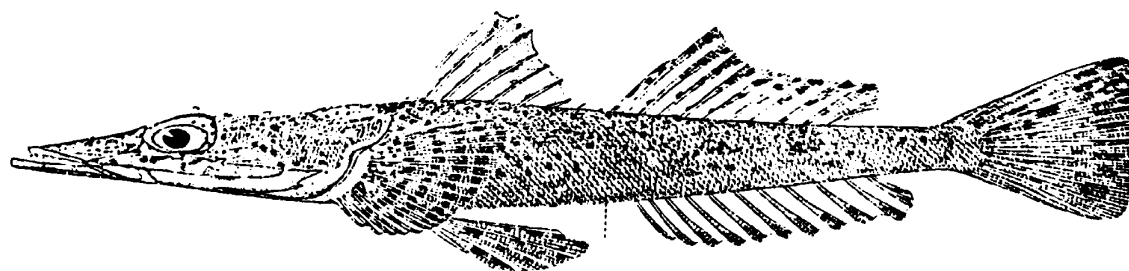


Fig. 62. Lateral aspect of *Ratabulus megacephalus*, type species of the genus (from Matsubara and Ochiai 1955).

Material examined. *Ratabulus megacephalus*: HUMZ 49470 (188mm), fish market, Mimase, Kouchi, Japan, 17 Nov. 1975; HUMZ 49396 (188mm), fish market, Mimase, Kouchi, Japan, 15 Nov. 1975; HUMZ 62600-62601 (2, 181-215mm), fish market, Mimase, Kouchi, Japan, 23. March 1977; NSMT-P 828 (103mm), Enoura, Izu Peninsula, Japan (35°03'N, 138°54'E), date unknown.

Genus *Grammoplites* Fowler, 1904

Grammoplites Fowler, 1904: 550 (type species: *Cottus scaber* Linnaeus, 1758).

Diagnosis. Dorsal surface of head with tubercles present (*G. suppositus*) or absent (*G. knappi* and *G. scaber*); suborbital ridge usually with four or more distinct spines; all lateral line scales with a distinct spine and a single opening to the exterior (Fig. 49B); iris lappet usually simple (rarely slightly bilobed in *G. suppositus*); ocular and interopercular flaps absent; sensory tubes on cheek region not developed (Fig. 53A).

Remarks. The genus *Grammoplites* included 5 species according to Knapp (1986) and Imamura and Amaoka (1994), but such a grouping was not monophyletic. Only *G. scaber* (Linnaeus, 1758) (= type species) (Fig. 63) and *G. suppositus* (Troschel, 1840) were concluded as being monophyletic. In addition, *G. knappi* Imamura and Amaoka, 1994, is also considered to be a member of this genus, since it bears all the diagnostic external features (Imamura and Amaoka 1994; pers. obs.), although its internal morphology was not examined. As for the other species previously assigned to *Grammoplites*, *Platycephalus gruvelli* Pellegrin, 1905 and *P. portuguesus* Smith, 1953 are removed to *Solitas* and *Rogadius*, respectively.

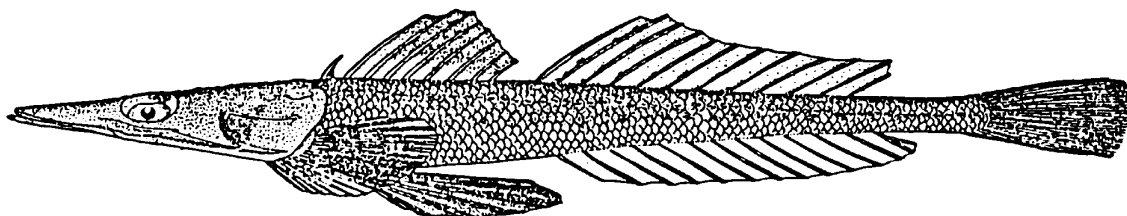


Fig. 63. Lateral aspect of *Grammoplites scaber*, type species of the genus (from Chu *et al.* 1962).

Material examined. *Grammoplites knappi*: HUMZ 109614 (holotype, 210mm), female, off Sarawak, Borneo Island, 1-8 Dec. 1970; CAS 80623 (3 paratypes, 190-208mm), Gulf of Thailand (12° 15'00"N, 100° 16'00"E), ca. 24-26 m, 6-9 Aug. 1960; CAS 80624 (2 paratypes, 217-227mm), Gulf of Thailand (12° 39'25"N, 100° 15'45"E), 33 m, 13 Dec. 1960; HUMZ 128622-128624 (3 paratypes, 203-225mm), acquired from a fish processing factory, Pak-nam, Bangkok, Thailand, 29 Aug. 1991; NSMT-P 45836-35838 (3 paratypes, 196-214mm), acquired from a fish processing factory, Pak-nam, Bangkok, Thailand, 21 Aug. 1991; URM-P 29670, 29678, 29691 (3 paratypes, 170-217mm), collected with HUMZ 128622-128624; USNM 324970 (paratype, 216mm), acquired from a fish market, Bangkok, collected from the Gulf of Thailand (12° 09'-12° 18'N, 100° 21'-100° 22'E), 7-11 Apr. 1961; USNM 327280 (paratype, 188mm), Gulf of Thailand (12° 39'15"N, 100° 15'45"E), 33 m, 13 Dec. 1960; CAS 134032 (143mm), Hainan Island, China, 1932; URM-P 29669, 29671-29674,

29677, 29679-29683, 29686, 29688-29689 (14, 182-235mm), collected with NSMT-P 45836-45838.

G. scaber: CAS 82625 (20, 146-214mm), Thailand (13° 20'00"N, 100° 45'15"E), 1-10 m, 7-9 Dec. 1957; FUMT-P 8538 (173mm), fish market, Yanawa, Bangkok, Thailand, 16 Feb. 1985; URM-P 29702 (127mm), fish market, Phuket, Thailand, 2 Oct. 1991; URM-P 29725-29727 (3, 161-193mm), fish market, Phuket, Thailand, 8 Dec. 1991; URM-P 29730 (243mm), Phuket, Thailand, 12 Dec. 1991; FUMT-P (unregistered, 142mm), Thailand, date unknown.

G. suppositus: HUMZ 135124-135125 (2, 109-131mm), Red Sea, Massawa, Ethiopia (ca. 15° 09'N, 40° 31'E), 19 Sep. 1971; HUMZ 135126-135129 (4, 136-196mm), Cochin, India, 30-50 m, 2 May 1980.

Genus *Cociella* Whitley, 1940

Cocius Jordan and Hubbs, 1925: 286 (type species: *Platycephalus crocodilus* Tilesius, 1812).

Cociella Whitley, 1940: 243 (substitute for *Cocius* Jordan and Hubbs, 1925, preoccupied).

Diagnosis. Suborbital ridge with 3 spines, one in front of eye (preorbital spine), second below middle of eye, third below rear margin of eye (additional spines may or may not be present posterior to eye, according to Knapp [1996]) (Fig. 12B); lateral line scales with one exterior opening posteriorly; ocular flaps absent; sensory tubes on cheek region not developed.

Remarks. Recently, Knapp (1996) included five species in *Cociella*: viz. *C. crocodila* (Tilesius, 1812) (= type species) (Fig. 64), *C. punctata* (Cuvier, 1829), *C. hutchinsi* Knapp, 1996, *C. heemstrai* Knapp, 1996 and *C. somaliensis* Knapp, 1996. Of these, *C. punctata*, *C. heemstrai* and *C. somaliensis* have an interopercular flap, which is considered herein as supporting clade N3, while *C. crocodila*, which was the only species of the genus examined internally in this study, does not have one. Knapp's (1996) definition of the genus is provisionally followed here, but further study is necessary to define the generic limits, as well as to resolve the trichotomy of *Grammoplites*, *Cociella* and clade N3.

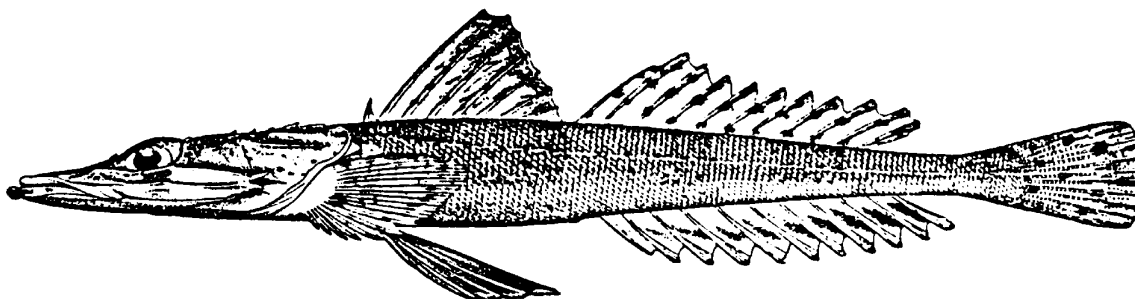


Fig. 64. Lateral aspect of *Cociella crocodila*, type species of the genus (from Jordan and Richardson 1908).

Material examined. *Cociella crocodila*: HUMZ 37356 (141mm), fish market,

Mimase, Kouchi, Japan (?), date unknown; HUMZ 44408 (142mm), Hyogo, Japan, 18 May 1954; HUMZ 59969 (131mm), off Murakami, Niigata, Japan, 23 Oct. 1976.

C. punctata: NSMT-P 29286 (73mm), Yaeyama Group, Ryukyu Islands, Japan, 27 Aug. 1974.

Genus *Cymbacephalus* Fowler, 1938

Cymbacephalus Fowler, 1938: 90 (type species: *Platycephalus nematophthalmus* Günther, 1860).

Diagnosis. Dorsal surface of head with spines only; suborbital ridge with one or two spines (Fig. 12C); lateral line scales with a single opening to exterior; iris lappet long and branched; ocular flaps present (*C. nematophthalmus* and *C. beauforti*) or absent (*C. staigeri*); large interopercular flap present; a pit present behind eye (Fig. 50B); sensory tubes on cheek region absent or weakly developed.

Remarks. Although Knapp (1973) treated *Cymbacephalus* as a subgenus of *Platycephalus*, the former is justifiably recognized at the generic level owing to its position in the phylogenetic framework of Platycephalidae.

At present, the genus includes three species, *Cymbacephalus beauforti* (Knapp, 1973), *C. nematophthalmus* (Günther, 1860) (= type species) (Fig. 65) and *C. staigeri* (Castelnau, 1875).

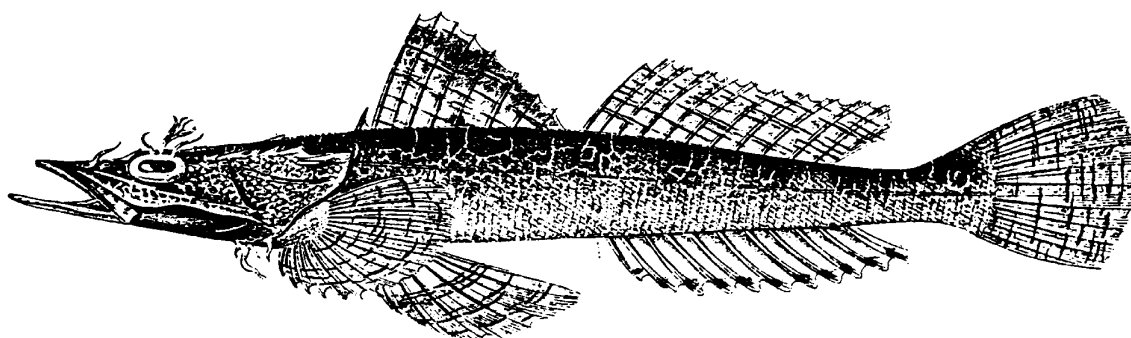


Fig. 65. Lateral aspect of *Cymbacephalus nematophthalmus*, type species of the genus (from Bleeker 1875-1878).

Material examined. *Cymbacephalus beauforti*: HUMZ 48224 (428mm), Ishigaki Island, Japan, 26 Apr. 1974.

C. staigeri: HUMZ 135139 (271mm), Western Australia (17° 04'–17° 05'S, 121° 37.5'E), 1 Oct. 1979.

Genus *Kumococius* Matsubara and Ochiai, 1955

Kumococius Matsubara and Ochiai, 1955: 89 (type species: *Insidiator detrusus* Jordan and Seale, 1905 [junior synonym of *Platycephalus rodericensis* Cuvier, 1829]).

Diagnosis. Dorsal surface of head with spines and tubercles (Fig. 16); suborbital

ridge usually with four or more distinct spines (Fig. 12D); pectoral fin concave posteriorly; lateral line scales with an exterior opening posteriorly (Fig. 49A); iris lappet simple or bilobed; ocular flaps absent; interopercular flap present; sensory tubes on cheek region not developed; swimbladder present.

Remarks. Jordan and Seale (1905) originally described *Insidiator detrusus* from a single specimen collected from a fish market in Hong Kong. Although Knapp (1992) considered the species to be a junior synonym of *Platycephalus rodericensis* Cuvier, 1829, no reasons were given. In this study, examination of the holotype of *I. detrusus* and 15 specimens of *P. rodericensis* collected from Thailand, disclosed that they had in common an interopercular flap, a simple broad iris lappet (rarely weakly bilobed in *P. rodericensis*), an exterior opening on the posterior margin of the lateral line scales, a posteriorly concave pectoral fin with a dark margin and tubercles on the dorsal surface of head (Fig. 66). Furthermore, there were no significant differences in counts and proportional measurements (Table 2). Accordingly, Knapp's (1992) synonymy is followed here.

Matsubara and Ochiai (1955) established a new genus, *Kumococius*, characterized by the absence of a flap on the anterior nostril, based on *Insidiator detrusus*. However, their grounds were erroneous, because the holotype of this species has a flap on the anterior nostril (Jordan and Seale 1905; pers. obs.). In addition, the flap was present on one side only in two specimens of *P. rodericensis* examined here, which is clear evidence of intraspecific variation in this character.

Although this species had been regarded as a member of *Suggrundus* (Knapp 1984, 1992; Sainsbury *et al.* 1985; Paxton *et al.* 1989), Knapp (1996) removed it to *Kumococius* without reasons. According to the present analysis, it is not related to *S. meerdervoortii*, type species of *Suggrundus*. Therefore, *Kumococius* is adopted for *P.*

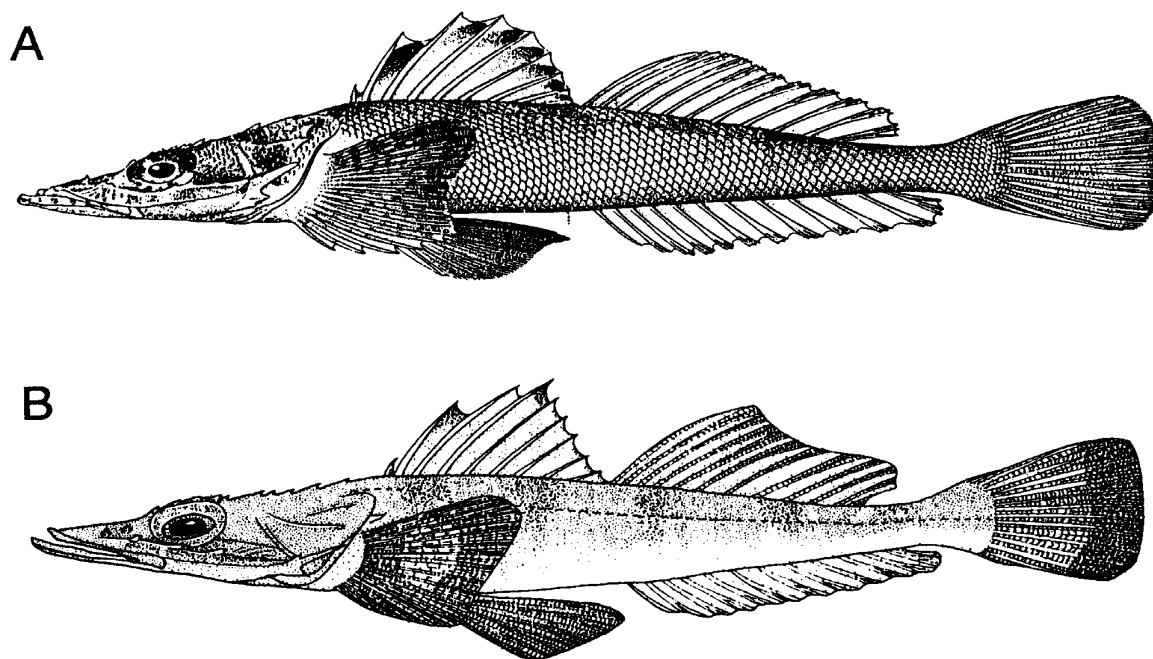


Fig. 66. Lateral aspect of holotype of *Insidiator detrusus* (from Jordan and Seale 1905) (A) and *Platycephalus rodericensis* (from Knapp 1984) (B).

Table 2. Counts and measurements of *Insidiator detrusus* (holotype) and *Platycephalus rodericensis*.

	<i>I. detrusus</i> (holotype)	<i>P. rodericensis</i> (n = 15)
SL (mm)	108	69–152
Counts		
Dorsal fin rays	I – VIII – 11	I – VIII – 11
Anal fin rays	12	12
Pectoral fin rays	2 + 11 + 6 = 19	2 + 11 – 14 + 4 – 6 = 19 – 21
Pelvic fin rays	1, 5	1, 5
Branched caudal fin rays	6(upper) + 6(lower)	6 + 5 – 6
Gill rakers	2 + 8 = 10	2 + 7 – 8 = 9 – 10
Measurements (% of SL)		
Head length	33.8	34.7–36.7
Length of first dorsal fin base	21.5	19.7–22.5
Length of second dorsal fin base	27.1	25.4–27.6
Length of anal fin base	33.0	29.3–32.6
Length of caudal peduncle	9.3	8.4–10.4
Depth of caudal peduncle	5.4	5.4–6.3
Snout length	10.2	9.9–10.8
Orbital diameter	8.9	9.3–10.2
Upper jaw length	13.1	12.8–14.2
Lower jaw length	21.6	22.1–23.2
Interorbital width	2.2	1.9–2.8
Pectoral fin length	18.2	16.7–19.8
Pelvic fin length	22.4	21.6–24.5
Caudal fin length	—	20.9–23.9
Length of first dorsal spine	2.5	3.0–4.2
Length of second dorsal spine	9.5	9.7–12.9
Length of first dorsal ray	13.4	14.1–15.9
Length of first anal ray	6.8	7.2–8.5

rodericensis, following Knapp (1996). The genus is distinguished from *Suggrundus*, as redefined in this study, in having no sensory tubes on the cheek region (vs. weakly or well developed ones in *Suggrundus*), lateral line scales with a single opening to the exterior (vs. two openings), pectoral fin concave posteriorly (vs. rounded) and swimbladder present (vs. absent).

The genus includes only one species, *K. rodericensis*.

Material examined. *Kumococius rodericensis*: CAS 109067 (formerly SU 9067, holotype of *Insidiator detrusus*, 108mm), fish market, Hong Kong, 1900; FUMT-P 8514-8520 (7, 103-152mm), off Prachuap Khiri Khan, Gulf of Thailand, 55 m (?), 4 July 1985; FUMT-P 8490 (121mm), off Surat Thani, Gulf of Thailand, 18 Feb. 1985; HUMZ 114960-114963 (4, 69-134mm), off Prachuap Khiri Khan, Gulf of Thailand, 55 m (?), 16-17, Feb. 1985; HUMZ 114965 (129mm), off Surat Thani, Gulf of Thailand,

Feb. 1985; FUMT-P (unregistered, 151mm), Gulf of Thailand (09°05'08"-09°00'09"N, 100°52'02"-100°54'01"E), 24 Nov. 1985.

Genus *Papilloculiceps* Fowler and Steinitz, 1956

Papilloculiceps Fowler and Steinitz, 1956: 283 (type species: *Platycephalus grandidieri* Sauvage, 1878 [junior synonym of *Pl. longiceps* Ehrenberg in Cuvier and Valenciennes, 1829]).

Diagnosis. Dorsal surface of head with spines only; a single suborbital spine usually present below posterior margin of eye; lateral line scales with two openings to exterior (Fig. 49E); iris lappet long and branched; ocular flap present (Fig. 50A); a large interopercular flap; sensory tubes on cheek region not developed.

Remarks. Only *Papilloculiceps longiceps* (Ehrenberg, 1829) (= type species) (Fig. 67) could be examined in this study, although Knapp (1986) recognized two species in the genus.

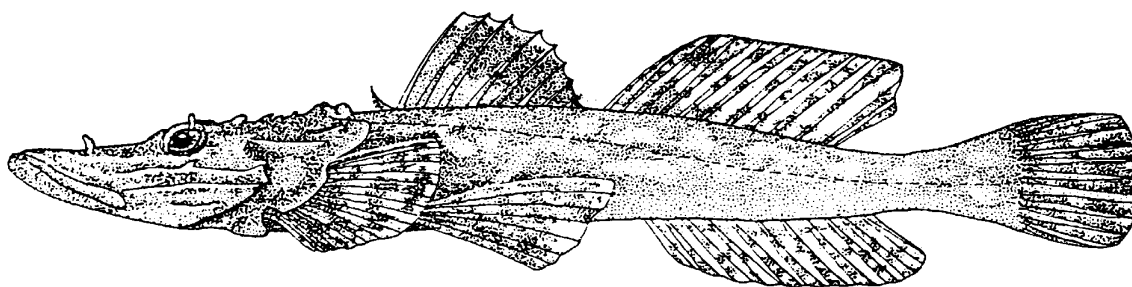


Fig. 67. Lateral aspect of *Papilloculiceps longiceps*, type species of the genus (from Knapp 1984).

Material examined. *Papilloculiceps longiceps*: HUMZ 113413-113414 (2, 91-127mm), Bazaruto, Mozambique, 1953.

Genus *Inegocia* Jordan and Thompson, 1913

Inegocia Jordan and Thompson, 1913: 70 (type species: *Platycephalus japonicus* Tilesius, 1812).

Levanaora Whitley, 1933: 95 (type species: *P. isacanthus* Cuvier, 1829 [junior synonym of *P. japonicus* Tilesius, 1812]).

Diagnosis. Dorsal surface of head with spines only; suborbital ridge usually with a spine below middle of eye and a second below rear margin of eye (sometimes with several additional small spines in *I. harrisii* [McCulloch 1914; L. W. Knapp, pers. comm.; pers. obs.]); preorbital spine absent; iris lappet long and branched; ocular flaps absent; sensory tubes on cheek region not developed.

Remarks. *Insidiator harrisii* McCulloch, 1914, *Platycephalus bosschei* Bleeker, 1860, *P. guttatus* Cuvier, 1829 and *P. japonicus* Tilesius, 1812 (=type species) (Fig. 68) have all been included in *Inegocia* (Matsubara and Ochiai 1955; Gloerfelt-Tarp

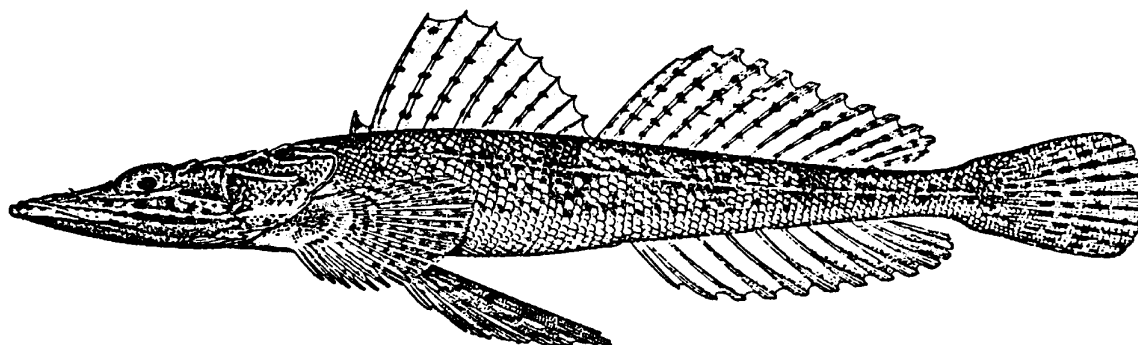


Fig. 68. Lateral aspect of *Inegocia japonica*, type species of the genus (from Jordan and Richardson 1908).

and Kailola 1984; Paxton *et al.* 1989; Keenan 1991). Provisional inclusion is continued here, although the internal morphologies of these species, except *I. japonica*, have not been examined in this study. That further examination is necessary, is indicated by *I. guttata*'s large broad interopercular flap (Matsubara and Ochiai 1955; Ochiai 1984; Nakabo 1993; pers. obs.), which is reminiscent of that in *Cymbacephalus*, *Papilloculiceps* and *Leviprora*.

Material examined. *Inegocia guttata*: NSMT-P 5772 (326mm), Senkai Bay, Tsushima, Nagasaki, Japan, 12-14 July 1968.

Inegocia harrisii: AMS I.34398038 (103mm), South Arm Channel, Port Clinton, Queensland, Australia (22° 33.23'-22° 33.49'S, 150° 45'E), 11 m, 25 Oct. 1993; HUMZ 135134 (178mm), Australia (13° 43.5'S, 128° 38.6'E), 62 m, 26 Dec. 1969.

Inegocia japonica: NSMT-P 3237 (3, 166-193mm), Shimonoseki, Yamaguchi, Japan, 11 Oct. 1961; NSMT-P 19059-19060 (3, 118-175mm), Kagoshima Bay, east coast of Satsuma Peninsula, Kagoshima, Japan (31° 22'N, 130° 35'E), 22 May 1980.

Genus *Suggrundus* Whitley, 1930

Insidiator Jordan and Snyder, 1900: 368 (type species: *Platycephalus rudis* Günther, 1880 [junior synonym of *P. meerdervoortii* Bleeker, 1860]).

Suggrundus Whitley, 1930: 26 (substitute for *Insidiator* Jordan and Snyder, 1900, preoccupied).

Lepotrudis Whitley, 1930: 27 (type species: *Platycephalus macracanthus* Bleeker, 1869).

Diagnosis. Dorsal surface of head with spines and tubercles; suborbital ridge usually with four or more distinct spines; lateral line scales with two openings to exterior (Fig. 49D); iris lappet bilobed or scalloped; ocular flaps absent; interopercular flap long or short (Fig. 53B); sensory tubes on cheek region weakly or well developed (Fig. 53B); swimbladder absent.

Remarks. Whitley (1930) also erected a new subgenus *Lepotrudis* in the present genus, designating *Platycephalus macracanthus* as the type species, although recent ichthyologists have not recognized it (Knapp 1984; Sainsbury *et al.* 1985; Chen and Shao 1993; Shao and Chen 1993). Whitley (1930) defined *Lepotrudis* as having the

following external characters: interorbital space less than vertical diameter of eye, anterior lateral line scales with a distinct spine, and an elongated upper preopercular spine. However, a narrow interorbit and spined lateral line scales are common characters in most platycephalids, and the last-mentioned of Whitley's characters is also found in other platycephalids: viz. *Platycephalus longispinis*, *Grammoplites suppositus* (Fig. 53A) and *Suggrundus cooperi*. Moreover, *P. macracanthus* could not be defined by apomorphic characters in this study. Therefore, it is regarded as a junior synonym of *Suggrundus*, rather than recognizing the poorly-defined *Lepotrudis*.

Suggrundus includes three species, *S. cooperi* (Regan, 1908), *S. macracanthus* (Bleeker, 1869) and *S. meerdervoortii* (Bleeker, 1860) (=type species) (Fig. 69). Although Knapp (1984) reported *S. cooperi* as lacking interopercular flaps, a small, blunt flap was apparent in one of the syntypes, as well as in an additional example of that species. *Suggrundus brevirostris* Shao and Chen, 1987 is a junior synonym of *Thysanophrys celebica* (Bleeker, 1854) (Chen and Shao 1993; Shao and Chen 1993). In addition, *Suggrundus longirostris* Shao and Chen, 1987 is also considered to be a member of the herein newly-defined *Thysanophrys* (see under "Remarks" for genus *Thysanophrys*).

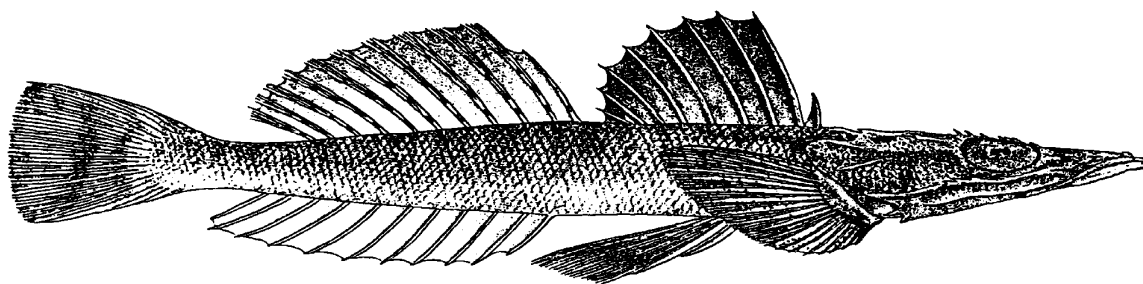


Fig. 69. Lateral aspect of *Suggrundus meerdervoortii*, type species of the genus (from Günther 1880).

Material examined. *Suggrundus cooperi*: BMNH 1908.3.23.204 (syntype, 124mm), Seychelles Group or Cargados Carajos, western Indian Ocean, 23 March 1908.

S. macracanthus: RMNH 5924 (2, holotype [123 mm] and non-type [86 mm]), Amboina (= Ambon), 1845; FUMT-P 8531 (137mm), off Pattani, Gulf of Thailand, 28 Feb. 1985; HUMZ 109615-109617 (3, 97-157mm), off Sarawak, Borneo Island, South China Sea, 1-8 Dec. 1970; FUMT-P (unregistered, 89mm), off Songkhla, Gulf of Thailand, 9 July 1985; FUMT-P (unregistered, 137mm), off Ko Samet, Gulf of Thailand, 9 Nov. 1985.

S. meerdervoortii: HUMZ 5452 (79mm), Yamaguchi, Japan, Aug. 1952; HUMZ 35453 (113mm), Mimase, Kouchi, Japan, 17 Nov. 1974; HUMZ 39515 (132mm), fish market, Mimase, Kouchi, Japan, 11 July 1973; HUMZ 47413 (150mm), fish market, Mimase, Kouchi, Japan, 6. Oct. 1972; HUMZ 49191, 49193-49194 (3, 113-185mm), Odawara, Kanagawa, Japan, Nov. 1975; HUMZ 49257-49258 (2, 111-184mm), Odawara, Kanagawa, Japan, 10. Nov. 1975; HUMZ 51861 (168mm), fish market, Mitani, Aichi, Japan, 250 m, 13 March 1976; HUMZ 51904 (191mm), Sado Island, Niigata, Japan, 20 Jan. 1976; HUMZ 52259-52260 (2, 184-188mm), Mitani, Aichi, Japan, 26 March 1976; HUMZ 52579 (170mm), Sado Island, Niigata, Japan, 7 Feb. 1976; HUMZ 53576-53577 (2, 97-169mm), Hashidate, Ishikawa, Japan, 2 July 1976;

HUMZ 59143 (189mm), off Futami, Sado Island, Niigata, Japan, 23 Sep. 1976; HUMZ 59183 (182mm), off Mano, Sado Island, Niigata, Japan, 80 m, 23 Sep. 1976; HUMZ 59967-59968, 59970 (3, 82-98mm), off Murakami, Sado Island, Niigata, Japan, 23 Oct. 1976; HUMZ 63631 (134mm), off Iwafune, Niigata, Japan, 14 Apr. 1977; HUMZ 107039 (190mm), Shizuoka, Japan, 12 Nov. 1985; HUMZ 135097 (44mm), off Yamagata, Japan, 14 Sep. 1994.

Genus *Eurycephalus* gen. nov.

Type species. *Thysanophrys arenicola* Schultz, 1966.

Etymology. The name *Eurycephalus* is derived from Greek, in reference to the broad head. The gender is masculine.

Diagnosis. Dorsal surface of head with spines only (Figs 70, 71); suborbital ridge usually with four or more distinct spines (Figs 70, 71); basisphenoid posteriorly attached only to prootic; lateral line scales with two exterior openings posteriorly; iris lappet finger-like or branched; ocular flaps absent (*E. arenicola* and *E. otaitensis*) or present (*E. carbunculus*); interopercular flap absent; sensory tubes on cheek region weakly developed.

Remarks. Both *Thysanophrys arenicola* Schultz, 1966 (Figs 70, 71) and *Cottus otaitensis* Parkinson, 1829 have to date been included in the genus *Thysanophrys* (Knapp 1984, 1986; Paxton *et al.* 1991; Imamura *et al.* 1995). However, based on the interrelationships of the platycephalids, they are here removed to a new genus. *Platycephalus carbunculus* Valenciennes, 1833, which has likewise been considered a member of *Thysanophrys* (Knapp 1984; Imamura *et al.* 1995), is also tentatively included in the new genus, because it has only weakly developed sensory tubes on the cheek region, unlike *Thysanophrys* as redefined here.

Material examined. *Eurycephalus arenicola*: HUMZ 135114-135122 (9, 57-182mm), Philippines, June 1978; WAM P. 28538-013 (2, 102-131mm), Coral Sea (16°31'S, 147°50'E), 15-18 m, 19 Nov. 1985; WAM P. 28541-026 (113mm), Coral Sea (16°31'S, 147°50'E), 12-14 m, 20 Nov. 1985; WAM P. 29642-017 (2, 57-150mm), Coral Sea (17°25'S, 150°48'E), 9-10 m, 15 Nov. 1987; WAM P. 30366-002 (2, 91-100mm), Madang, Papua New Guinea (05°10'S, 145°50'E), 15-17 m, 1 Nov. 1991; WAM P.

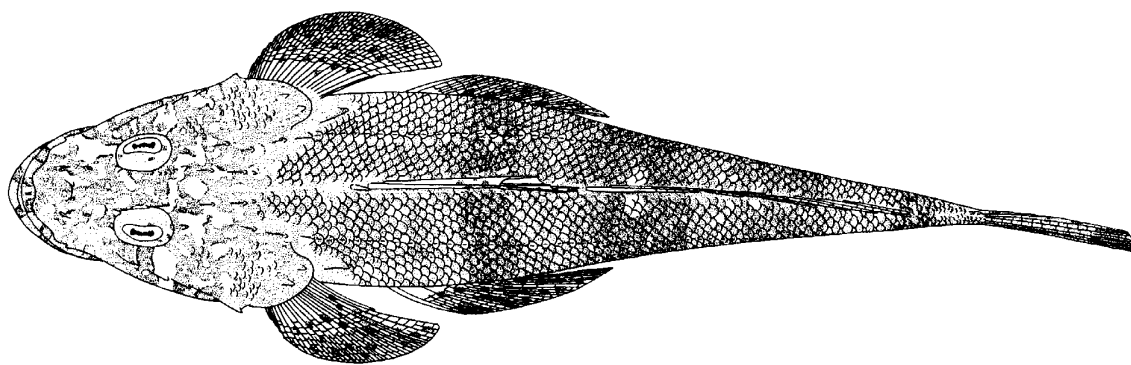


Fig. 70. Dorsal aspect of *Eurycephalus arenicola*, type species of the genus, WAM P.29642-017, 150mm SL.

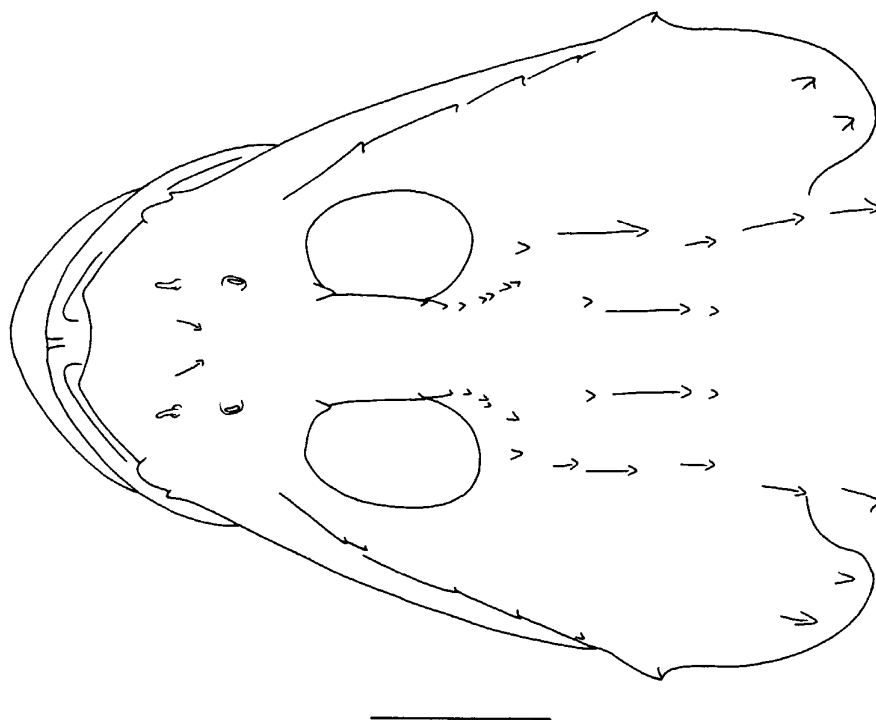


Fig. 71. Dorsal aspect of head region of *Eurycephalus arenicola*, type species of the genus, WAM P.29642-017, 150mm SL. Scale indicates 10mm.

30622-005 (78mm), Madang, Papua New Guinea (05°09'00"S, 145°50'00"E), 11-16 m, 24 Jan. 1993.

E. carbunculus: MNHN 6875 (holotype, 128mm), Bombay, India, date unknown.

E. otaitensis: BMNH 1876.6.5.1 (holotype of *Platycephalus variolosus* Günther, 1876, 132mm), Samoa, 5 June 1876; RMNH 5968 (holotype of *Platycephalus malayanus* Bleeker, 1853, 77mm), Sumatra, date unknown; NSMT-P 46965 (2, 146-182mm), Miyake Island (ca. 34°05'N, 139°30'E), Izu Islands, Japan, 10 m, 27 Aug. 1980; NSMT-P 46966 (2, 141-156mm), Ani Island (ca. 27°05'S, 142°15'E), Chichijima Group, Ogasawara Islands, Japan, 22 July 1991; NSMT-P 46967 (131mm), Ani Island, Chichijima Group, Ogasawara Islands, Japan, 2 June 1992; WAM P. 27824-080 (5, 69-126mm), Manus Island (01°58'S, 147°23'E), Papua New Guinea, 19-20m, 4 Oct. 1982.

Genus *Thysanophrys* Ogilby, 1898

Thysanophrys Ogilby, 1898: 40 (type species: *Platycephalus cirronasus* Richardson, 1848).

Diagnosis. Dorsal surface of head with spines only; suborbital ridge usually with four or more distinct spines (absent in *T. cirronasa*) (Fig. 12E); basisphenoid posteriorly attached to prootic and pterosphenoid; lateral line scales with two exterior openings posteriorly (Fig. 49F); iris lappet long or short, branched; ocular flap(s) present (one in *T. armata* and *T. celebica*, many in *T. cirronasa*) or absent (*T.*

chiltonae and *T. longirostris*); interopercular flap absent; well developed sensory tubes completely covering cheek region.

Remarks. This genus includes *Thysanophrys armata* (Fowler, 1938), *T. chiltonae* Schultz, 1966 and *T. cirronasa* (Richardson, 1848) (= type species) (Fig. 72). *Platycephalus celebicus* Bleeker, 1854 is also considered as most likely belonging to *Thysanophrys*, because it conforms to all of the diagnostic characters, except attachment of the basisphenoid, which could not be examined in this study. *Suggrundus longirostris* Shao and Chen, 1987, which has "a big interopercle flap," according to its original description, is also a likely member of the present genus, since such a flap is otherwise found only in *T. chiltonae*. However, some generically diagnostic features of *S. longirostris* are unclear in the original description by Shao and Chen (1987).

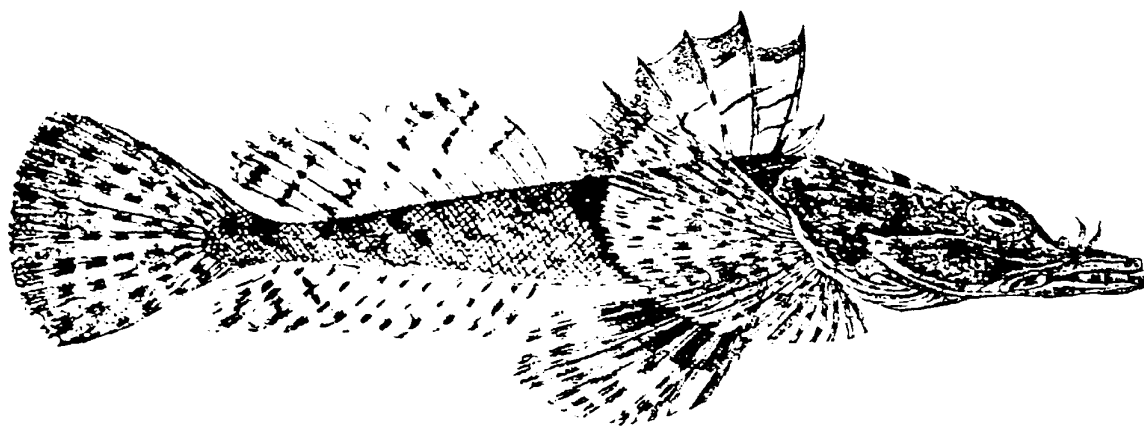


Fig. 72. Lateral aspect of *Thysanophrys cirronasa*, type species of the genus (from Scott *et al.* 1980, based on Richardson 1848).

Material examined. *Thysanophrys celebica*: HUMZ 135111 (94mm), Thailand, 8 May 1966.

T. chiltonae: NSMT-P 35570 (175mm), Sakinoue, Oshima Straits, Amami-oshima Island, Ryukyu Islands, Japan (28° 11.2'N, 129° 16'E), 13 Sep. 1989; NSMT-P 46967 (2, 132-153mm), Miyake Island, Izu Islands, Tokyo, Japan, 5 May 1979; WAM P 27824-080 (76mm), Manus Island (01° 58'S, 147° 23'E), Papua New Guinea, 19-20 m, 4 Oct. 1982.

T. cirronasa: CSIRO CA 3693 (182mm), Great Australian Bight (32° 30'S, 126° 43'E), 36 m, 1 Dec. 1981.

Genus *Solitas* gen. nov.

Type species. *Platycephalus gruvelli* Pellegrin, 1905.

Etymology. The genus name *Solitas* is derived from Latin, in reference to the isolated distribution of the type species. The gender is feminine.

Diagnosis. Dorsal surface of head with spines only (Fig. 74); suborbital ridge usually with four or more distinct spines (Figs 12F, 73, 74); lateral line scales with two exterior openings and distinct spines, without ctenii posteriorly (Fig. 49C); iris lappet weakly bilobed; ocular and interopercular flaps absent; sensory tubes on cheek

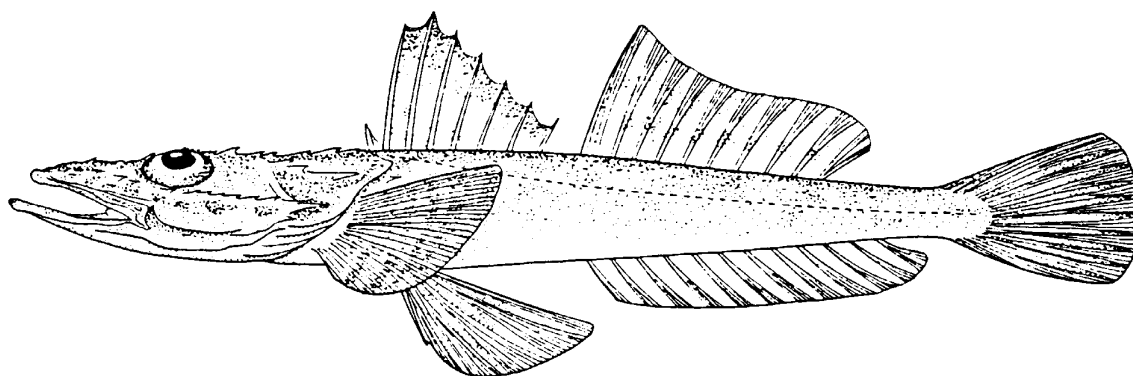


Fig. 73. Lateral aspect of *Solitas gruveli*, type species of the genus (from Knapp 1981).

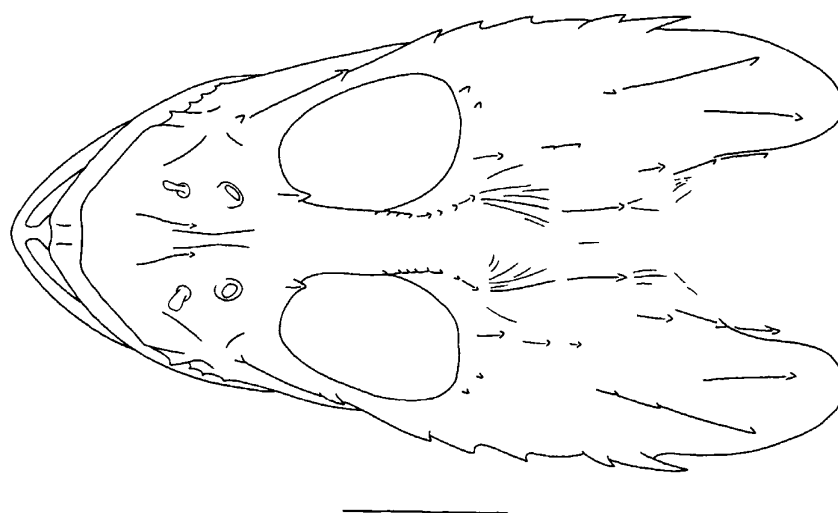


Fig. 74. Dorsal aspect of head region of *Solitas gruveli*, type species of the genus, BMNH 1914.2.2, 133mm SL. Scales indicates 10mm.

region well developed.

Remarks. *Platycephalus gruveli* Pellegrin, 1905 has been included in the genus *Grammoplites*, because of its having all lateral line scales with a distinct spine, such having been regarded as a diagnostic character of the genus since its inception (Knapp 1981; Imamura and Amaoka 1994). Judging from the phylogenetic analysis, *P. gruveli* is not closely related to *G. scaber*, type species of *Grammoplites*, and a new genus is necessary for its accommodation. *Solitas* is easily distinguished from *Grammoplites* in having the lateral line scales with two exterior openings (vs. one in *Grammoplites*) and lacking posterior ctenii (vs. with ctenii), in addition to having well-developed sensory tubes on the cheek region (vs. not developed). It is also separable from "*G.*" *portuguesus* in having several spines on the suborbital ridge (vs. serrations only).

Solitas includes only one species, *S. gruveli*, at present.

Material examined. *Solitas gruveli*: BMNH 1914.2.22 (2, 106-133mm), Lagos, western coast of Africa, 2 Feb. 1914.

Genus *Onigocia* Jordan and Thompson, 1913

Onigocia Jordan and Thompson, 1913: 70 (type species: *Platycephalus macrolepis* Bleeker, 1854).

Wakiyus Jordan and Hubbs, 1925: 286 (type species: *P. spinosus* Temminck and Schlegel, 1842).

Diagnosis. Dorsal surface of head with spines only (Fig. 17); suborbital ridge serrated (Fig. 12G); body scales large; lateral line scales about 40 or fewer, with two exterior openings; iris lappet short, branched or scalloped; ocular flap present (*O. macrolepis*, *O. spinosa* and *O. grandisquama*) or absent (*O. pedimacula* and *O. oligolepis*); interopercular flap absent; sensory tubes on cheek region well developed.

Remarks. Matsubara and Ochiai (1955) and Knapp (1986) assigned the following species to *Onigocia*: *Platycephalus grandisquama* Regan, 1908, *P. macrolepis* Bleeker, 1854 (= type species) (Fig. 75), *P. oligolepis* Regan, 1908, *P. pedimacula* Regan, 1908 and *P. spinosa* Temminck and Schlegel, 1842. All of these species satisfy the diagnostic characters of the genus and are accepted here.

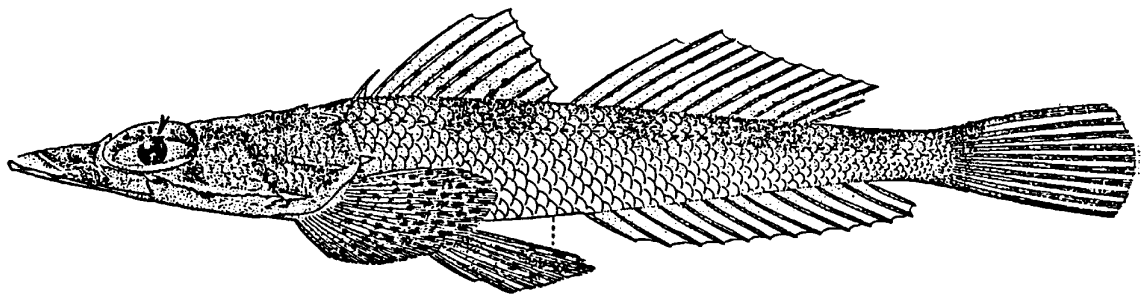


Fig. 75. Lateral aspect of *Onigocia macrolepis*, type species of the genus (from Chu *et al.* 1962).

Material examined. *O. grandisquama*: BMNH 1908. 3. 23. 209 (holotype, 54mm), Amirante Islands, Seychelles, western Indian Ocean, 23 March, 1908.

O. macrolepis: HUMZ 35464 (82mm), Mimase, Kouchi, Japan, 17 Nov. 1974; HUMZ 48181 (76mm), fish market, Kouchi, Japan, 5 Oct. 1972; HUMZ 49469 (78mm), fish market, Mimase, Kouchi, Japan, 17 Nov. 1975; HUMZ 65559 (95mm), Ishikawa, Japan (36° 19.5'N, 136° 08'E), 75-82m, 1 June 1977; HUMZ 79918-79919 (2,60-88mm), Kumanonada, Mie, Japan, 85 m, 11 Dec. 1978; HUMZ 79976 (105mm), Kumanonada, Mie, Japan, 290 m, 12 Dec. 1978; HUMZ 35076, 36475, 37223, 74838-74839, 74842, 75333, 75335 (8, 57-102mm), data unknown; HUMZ109310, 109331 (2,73-78mm), fish market, Mimase, Kouchi, Japan, 8 Nov. 1985; NSMT-P 29895, 28897 (9, 56-82mm), Mogi, Nagasaki, Japan, 6 Dec. 1965.

O. oligolepis: CSIRO CA2341-2342 (2, 68-72mm), northeast of Montebello Islands, Australia (20° 01.0'-20° 03.0'S, 115° 57.0'-115° 58.0'E), 80 m, 2 Dec. 1979; CSIRO CA1867, 2357, 2358-2360 (5, 77-96mm), east of Barrow Islands, Australia (20° 46.0'-20° 48.0'S, 115° 59.0'-116° 00.0'E), 19.0-22.0 m, 1 Dec. 1979.

O. pedimacula: BMNH 1901.12.31.45 (holotype, 45mm), Kolumadulu Atoll, Maldives, Indian Ocean, 31 Dec. 1901.

O. spinosa: CSIRO B2125 (50mm), west of Darwin, Australia (12° 16.0'-12° 18.0'S, 124° 03.0'-124° 05.0'E), 82.0 m, 16 July 1980; HUMZ 35832, 36413, 37470, 37512,

74829-74836 (12, 60-107mm), data unknown; HUMZ 71719 (86mm), fish market, Taiwan, 2 Feb. 1977; NSMT-P 4682-4683 (2, 51-84mm), off Jougasima, Miura Peninsula, Kanagawa, Japan, 8. Dec. 1968; NSMT-P 5698 (84mm), Senkai Bay, Tsushima, Nagasaki, Japan, 12-14 July 1968.

Genus *Ambiserrula* gen. nov.

Type species. *Insidiator jugosus* McCulloch, 1914.

Etymology. The new genus name *Ambiserrula* is derived from Latin, in reference to the finely serrated suborbital ridge. The gender is feminine.

Diagnosis. Dorsal surface of head with spines only (Fig. 77); suborbital ridge finely serrated (Figs 76, 77); lateral line scales about 50, with two exterior openings posteriorly; iris lappet long branched; ocular flaps absent; interopercular flap present; sensory tubes on cheek region well developed.

Remarks. Although Paxton *et al.* (1989) included *Insidiator jugosus* in the genus *Suggrundus*, the former has no close relationships with members of that genus.

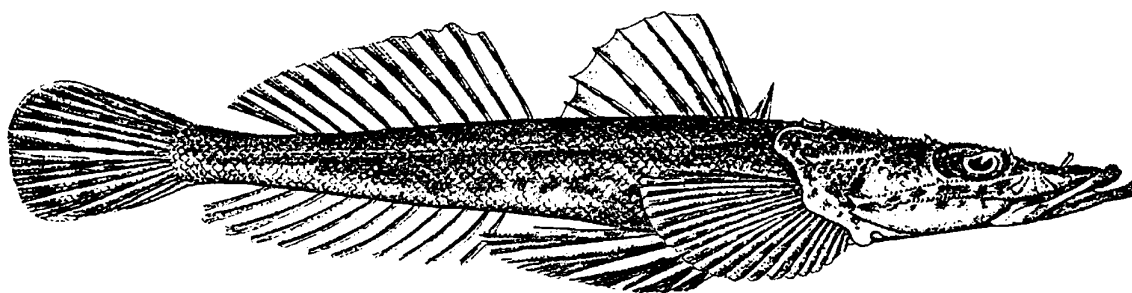


Fig. 76. Lateral aspect of *Ambiserrula jugosa*, type species of the genus (from McCulloch 1914).

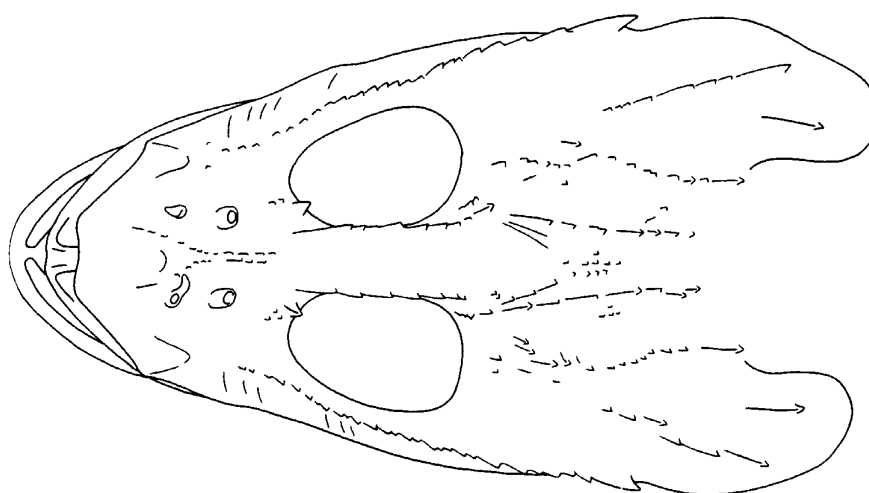


Fig. 77. Dorsal aspect of head region of *Ambiserrula jugosa*, type species of the genus, AMS I.256630-012, 121mm SL. Scale indicates 10mm.

Accordingly, a new (monotypic) genus is established for *I. jugosus*. *Ambiserrula jugosa* resembles species of *Onigocia* and the herein redefined *Rogadius*, in having a finely serrated suborbital ridge. However, it can be easily distinguished from those genera, having about 50 lateral line scales (vs. about 40 or fewer in *Onigocia*), an interopercular flap (vs. absent in *Onigocia* and *Rogadius*), the head with only small spines along the ridges (vs. spines and tubercles in *Rogadius*), and a long, branched iris lappet (vs. short and branched, or scalloped in *Onigocia*, and bilobed or scalloped in *Rogadius*). *Ambiserrula* also differs from *Suggrundus*, which usually has four or more spines on the suborbital ridge and a bilobed or scalloped iris lappet.

Material examined. *Ambiserrula jugosa*: AMS I.255663-012 (2, 102-121mm), New South Wales, Australia (29°31'-29°34'S, 153°25'-153°28'E), 49-53 m, 24 March 1985; AMS I.25771-001 (168mm), New South Wales, Australia (33°S, 151°E), 5 May 1981; AMS I.34361-013 (125mm), Queensland, Australia (22°32.68'-22°38.28'S, 150°48.42'-150°49.12'E), 15 m, 23 Oct. 1993; AMS I.34505-004 (153mm), New South Wales, Australia (32°59'-33°01'S, 151°45'-151°47'E), 29-33m, 30 March 1993.

Genus *Rogadius* Jordan and Richardson, 1908

Rogadius Jordan and Richardson, 1908: 930 (type species: *Platycephalus asper* Cuvier, 1829).

Sorsogona Herre, 1934: 67 (type species: *S. serrulata* Herre, 1934 [junior synonym of *P. tuberculatus* Cuvier, 1829]).

Diagnosis. Dorsal surface of head with spines and tubercles; suborbital ridge finely serrated (Fig. 12H); one or several preocular spines present (Fig. 18); antrorse preopercular spine present (*R. asper*, *R. pristiger* and *R. serratus*) or absent (Fig. 23F); lateral line scales about 50, with two exterior openings; iris lappet bilobed or scalloped; ocular and interopercular flaps absent (Figs 51A, 53C); sensory tubes on cheek region well developed (Fig. 53C).

Remarks. The genus *Rogadius* was established by Jordan and Richardson (1908) as being characterized by an antrorse preopercular spine. However, recently Knapp (1987) described *R. patriciae*, which lacks the spine. On the other hand, *Sorsogona*, originally described by Herre (1934), has been considered as a valid genus, defined by more than two preocular spines (Knapp 1979, 1984, 1986; Knapp and Wongratana 1987). As a result of the present analysis, *Rogadius* (*sensu* Knapp 1987) is not here regarded as a monophyletic group, because it has no synapomorphies. Instead, a newly-defined *Rogadius*, for the former *Rogadius*, *Sorsogona* and "*Grammoplites*" *portuguesus*, is proposed, rather than the erection of a new genus solely for the poorly-defined *R. patriciae*.

Here regarded as a monophyletic grouping, the following species are included in *Rogadius*: *R. asper* (Cuvier, 1829) (= type species) (Fig. 78), *R. melanopterus* (Knapp and Wongratana, 1987), *R. nigripinnis* (Regan, 1905), *R. patriciae* Knapp, 1987, *R. portuguesus* (Smith, 1953), *R. prionotus* (Sauvage, 1873), *R. pristiger* (Cuvier, 1829), *R. serratus* (Cuvier, 1829) and *R. tuberculatus* (Cuvier, 1829). *Wakiyus welanderi* Schultz, 1966 also belongs to *Rogadius*, because it has a finely serrated suborbital ridge, several preocular spines, a bilobed iris lappet, no interopercular flap and about 50 lateral line scales (Schultz 1966; Gloerfelt-Tarp and Kailola 1984; Myers 1989).

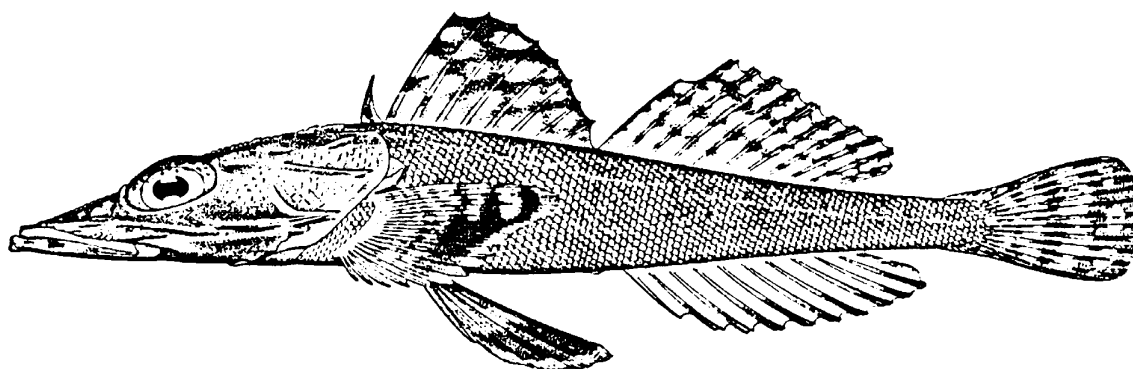


Fig. 78. Lateral aspect of *Rogadius asper*, type species of the genus (from Jordan and Richardson 1908).

Platycephalus polijodon Bleeker, 1853 is a junior synonym of *R. serratus*, as pointed out by Imamura and Amaoka (1996).

Material examined. *Rogadius asper*: HUMZ 49466 (140mm), fish market, Mimase, Kouchi, Japan, 17 Nov. 1975; HUMZ 62651 (142mm), fish market, Mimase, Kouchi, Japan, 3 March 1977; HUMZ 71649, 71658 (2, 67-109mm), fish market, Taiwan, 29 Oct. 1977; HUMZ 74823-74828(6, 85-131mm), fish market, Mimase, Kouchi, Japan (?), date unknown.

R. nigripinnis: HUMZ 135133 (154mm), Ras Hafan, Somalia, Indian Ocean (10°07'24"N, 51°31'12"E), 42 m, 6 Feb. 1987.

R. patriciae: HUMZ 6568-6569 (2, 142-184mm), Indian Ocean, Dec. 1962; HUMZ 135136-135138 (3, 140-161mm), Indian Ocean (ca. 19°38'S, 116°25'E), 70-94 m, 14 Oct. 1979.

R. prionotus: HUMZ 135131 (147mm), Gulf of Oman (23°47.6'-23°50'N, 57°57'-57°55'E), 18-20 m, 11 March 1977.

R. pristiger: CSIRO CA1860 (130mm), northeast of Montebello Island, Western Australia (20°03'S, 116°04'E), 62 m, 4 Nov. 1980; CSIRO H3306-12 (2, 95-117mm), off Shelburne, northwest of Saunders Island, Queensland, Australia (11°41'S, 143°05'E), 24.0 m, 14 Jan. 1993; CSIRO H3316-01 (125mm), Gulf of Carpentaria, west of Wepia, Queensland, Australia (12°37'S, 141°04'E), 45.0 m, 21 Jan. 1993; CSIRO H3361-06 (3, 111-120mm), west of Cape York Peninsula, Queensland, Australia (11°10'S, 141°04'E), 34.0 m, 4 Feb. 1993; MNHN 6855 (syntype, 119mm), New Guinea, date unknown; MNHN 6856 (syntype, 108mm), Celebes, date unknown; MNHN 4529 (101mm), Celebes, date unknown; HUMZ 131413 (123mm), New Guinea, 6 Dec. 1969; HUMZ 131415 (110mm), New Guinea, 25 Dec. 1969.

R. serratus: MNHN 6847 (holotype, 130mm), Trincomalee, Ceylon, date unknown; RMNH 5992 (2, including holotype of *Platycephalus polijodon* from Java, 95mm), date unknown.

R. tuberculatus: HUMZ 112092-112093, 112096, 112098 (4, 57-96mm), Gulf of Thailand, 5 July 1985; HUMZ 112101 (51mm), off Pran Buri, Gulf of Thailand, 5 July 1985; HUMZ 112116 (78mm), off Kochian (?), Gulf of Thailand, 26 m, 24 Feb. 1985.

Incertae sedis: genus ***Leviprora*** Whitley, 1931

Leviprora Whitley, 1931b: 237 (type species: *Platycephalus inops* Jenyns, 1840).
Cumbel Whitley, 1952: 32 (type species: *P. haacki* Steindachner, 1884 [junior synonym of *P. inops*]).

Diagnosis. Dorsal surface of head lacking spines and tubercles; iris lappet long, branched; ocular flaps absent; wide interopercular flap present; pit behind eye absent; sensory tubes on cheek region not developed.

Remarks. The genus *Leviprora* was established by Whitley (1931b) on the basis of *Platycephalus inops* Jenyns, 1840 (Fig. 79). The phylogenetic position of this genus could not be determined herein, because no specimens were available for dissection. However, *L. inops* may be related to *Cymbacephalus*, owing to its having the following characters: two separated tooth plates on the prevomer, about 50 lateral line scales, undeveloped sensory tubes on the cheek region, a wide interopercular flap, and a long, branched iris lappet (pers. obs.). These features occur in all species of *Cymbacephalus*, except *C. nematophthalmus*, in which the sensory tubes are weakly developed. The relationships determined using allozyme electrophoresis by Keenan (1991) support this hypothesis.

Leviprora includes only *L. inops*.

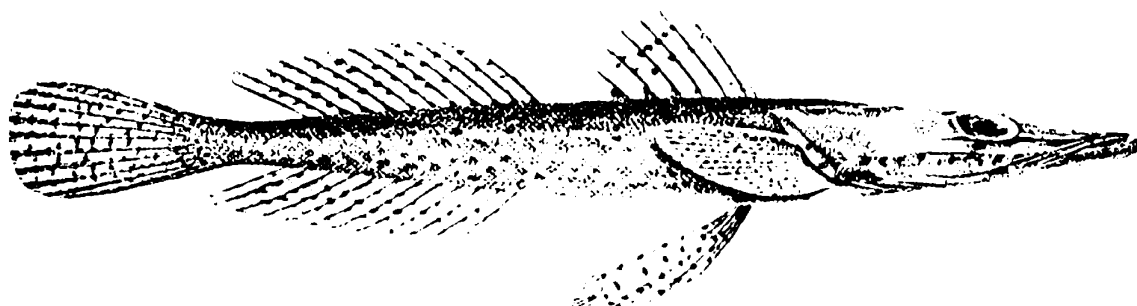


Fig. 79. Lateral aspect of *Leviprora inops*, type species of the genus (from Scott *et al.* 1980, based on Steindachner 1884).

Material examined. *Leviprora inops*: CSIRO C2365 (292mm), Rockingham, Western Australia (32° 17'S, 115° 43'E), 1953.

Summary

The present study was made to elucidate the phylogenetic relationships of Platycephalidae and its related taxa, and to review the higher taxonomy of the platycephalids on the basis of those interrelationships. Cladistic methodology was adopted for reconstruction of the relationships. Character polarities were determined using the two-step procedure of Maddison *et al.* (1984). Initially, platycephalid and scorpaenoid relationships were analyzed in order to determine the outgroups and character polarities for platycephalids. Secondly, the relationships of platycephalids and their sister group, comprising triglids, peristediids and hoplichthyids, were

deduced. Conclusions are summarized below.

(1) Platycephaloidei and Scorpaenoidei comprise a monophyletic group, supported by two characters, presence of a backwardly-directed opercular spine and an extrinsic muscle derived from the hypaxial.

(2) Platycephaloidei and *Plectrogenium*, the triglids and the peristediids are monophyletic, having a posterior pelvic fossa, which is an autapomorphic character in the platycephaloids and scorpaenoids. *Bembradium* and *Plectrogenium* constitute a monophyletic group, which divided initially from the other clade. Next, *Parabembras*, followed by *Bembras*, branched off the second clade. Platycephaloidei was redefined so as to include the former Platycephaloidei, *Plectrogenium*, Triglidae and Peristediidae.

(3) Platycephalidae has a sister group, including the triglids, peristediids and hoplichthyids, sharing 15 apomorphic characters. Platycephalidae and its sister group have 4 synapomorphies. The Peristediidae and Hoplichthyidae constitute a monophyletic group supported by 8 synapomorphies.

(4) Platycephalidae is a monophyletic group having 6 synapomorphies. It contains two subfamilies, Platycephalinae, comprised of *Platycephalus* and *Elates*, and Onigociinae, including *Ratabulus*, *Grammoplites*, *Cymbacephalus*, *Cociella*, *Kumococius*, *Papilloculiceps*, *Inegocia*, *Suggrundus*, *Eurycephalus*, *Thysanophrys*, *Solitas*, *Onigocia*, *Ambiserrula*, *Rogadius* and *Leviprora*. *Eurycephalus*, *Solitas* and *Ambiserrula* are newly-defined genera.

Acknowledgments

I express my sincere gratitude to Prof. Kunio Amaoka (HUMZ) for his guidance during this study and critical reading of the manuscript. My special thanks go to Takashi Minoda (formerly Hokkaido University) and Assoc. Prof. Kazuhiro Nakaya (HUMZ) for criticism of the manuscript, and also to Stuart G. Poss (GCRL), James C. Tyler, G. David Johnson and Carole C. Baldwin (USNM), and Graham S. Hardy (Thames, New Zealand) for their advice and comments on the manuscript, and to Assoc. Prof. Mamoru Yabe (Laboratory of Physiology, Faculty of Fisheries, Hokkaido University) for his valuable advice on fish phylogeny and scorpaeniform morphology. I sincerely thank Leslie W. Knapp (USNM) for his gift and loan of materials and provision of taxonomic information and literature on platycephalids. I thank Gento Shinohara (NSMT) for analyzing the phylogenetic relationships presented in this study and for helpful advice regarding scorpaeniform phylogeny and morphology.

I am deeply indebted to the following for their gifts and/or loans of materials: Gerald R. Allen and Mark Cowan (WAM), G. Duhamel (MNHN), Martin F. Gomon (NMV), Phillip C. Heemstra (RUSI), Hitoshi Ida (FSKU), Tomio Iwamoto (CAS), Peter R. Last and Alastair Graham (CSIRO), Keiichi Matsuura (NSMT), Kenji Mochizuki (FUMT; now Natural History Museum and Institute, Chiba), M. J. P. van Oijen (RMNH), John R. Paxton and Mark McGrouther (AMS), Barry C. Russell and Rex Williams (NTM), the late Ethelwynn Trewavas, Nigel R. Merrett and Anne-Marie Hodges (BMNH), Harumi Yamada (FSFL; now Seikai National Fisheries Research Institute), Tetsuo Yoshino (URM) and Mitsuhiro Sakashita (Okinawa Kurumaebi [Prawn] Co., Ltd.).

I also express my thanks to Kaoru Kido (Ohma Town Office, Aomori), Shigeru

Shirai (Seikai National Fisheries Research Institute, Nagasaki), Toru Miki (Himeji City Aquarium), Kiyonori Nishida (Osaka Aquarium Ring of Fire), Minoru Ishida (Nansei National Fisheries Research Institute, Kouchi), Kunio Sasaki (BSKU), Tomoyuki Komai (Natural History Museum and Institute, Chiba) and Hiromitsu Endo (BSKU) for discussion and valuable advice, and to my friends Kouichi Hoshino, Fumihito Muto, Tomoki Shimokawa, Tomoaki S. Goto, Eiji Mihara, Keizou Yoshimura, Christian O. Nyako, Hajime Miyahara, Daisuke Tsutsui, Masahito Arai, Hirotake Shinohara and Tetsumi Takahashi for their support and encouragement. I am very grateful to the staff of IAI Girls' High School, Hakodate, for their patient understanding of the constraints imposed by the study, while I was teaching there.

Finally, this study could not have been completed without the understanding and assistance of my wife, Mayumi Imamura.

References

- Baldwin, C. C. and Johnson, G. D. 1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bulletin of Marine Science* 52: 240-283.
- Bleeker, P. 1875-1878. *Atlas ichthyologique des Indes Orientales Néerlandaises. Tome 9*. Frédéric Muller et C., Amsterdam, 80 pp., pls. 355-360, 363-420.
- Bloch, M. E. 1795. *Naturgeschichte der ausländischen Fische. 9*. J. Morino, Berlin, 192 pp.
- Branson, B. A. and Moore, G. A. 1962. The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. *Copeia* 1962: 1-108.
- Castelnau, F. L. 1872. Contributions to the ichthyology of Australia. No.1. The Melbourne fish market. *Proceedings of the Royal Zoological Acclimatization Society of Victoria* 1: 29-242.
- Chen, J. P. and Shao, K. T. 1993. A new record of flathead fish, *Rogadius patriciae* (Platycephalidae), from Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* 32: 153-156.
- Chu, Y. T. and eleven coauthors. 1962. *Fishes of the South China Sea*. Science Press, Peking, xxxi+1184 pp. (In Chinese.)
- Farris, J. A. 1970. Method for computing Wagner trees. *Systematic Zoology* 19: 83-92.
- Fitch, W. M. 1971. Toward defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology* 20: 406-416.
- Fowler, H. W. 1904. A collection of fishes from Sumatra. *Journal of the Academy of Natural Sciences of Philadelphia. Series 2* 12: 497-560.
- Fowler, H. W. 1935. South African fishes received from Mr. H. W. Bell-Marley in 1935. *Proceedings of the Academy of Natural Sciences of Philadelphia* 87: 361-408.
- Fowler, H. W. 1938. Description of new fishes obtained by the United States Bureau of Fisheries steamer "Albatross", chiefly in Philippine seas and adjacent waters. *Proceedings of the United States National Museum* 85: 31-135.
- Fowler, H. W. and Steinitz, H. 1956. Fishes from Cyprus, Iran, Iraq, Israel and Oman. *Bulletin of the Research Council of Israel* 5B: 260-292.
- Fraser, T. H. 1968. Comparative osteology of the Atlantic snooks (Pisces: *Centropomus*). *Copeia* 1968: 433-460.
- Fraser, T. H. 1972. Comparative osteology of the shallow water cardinal fishes [Perciformes: Apogonidae] with reference to the systematics and evolution of the family. *Ichthyological Bulletin* 34: 1-105, 44 pls.
- Fujita, K. 1990. *The caudal skeleton of teleostean fishes*. Tokai University Press, Tokyo, xii+897

- pp. (In Japanese with English summary.)
- Gill, T. 1888. On the classification of the mail-cheeked fishes. *Proceedings of the United States National Museum* 11: 567-592.
- Gloerfelt-Tarp, T. and Kailola, P. J. 1984. *Trawled fishes of southern Indonesia and northern Australia*. The Australian Development Assistance Bureau, the Directorate-General of Fisheries, Indonesia and the German Agency for Technical Cooperation, Jakarta, xvi+2pls.+406 pp.
- Gosline, W. A. 1966. The limits of the fishes family Serranidae, with notes on other percoids. *Proceedings of the California Academy of Sciences*. 4th Series 33: 91-112.
- Greenwood, P. H. and Lauder, G. V. 1981. The protractor pectoralis muscle and the classification of teleost fishes. *Bulletin of the British Museum (Natural History)*, Zoology 41: 213-234.
- Greenwood, P. H., Rosen, D. E., Weitzman, S. H. and Myers, G. S. 1966. Phyletic studies of teleostean fishes, with provisional classification of living forms. *Bulletin of the American Museum of Natural History* 131: 339-456.
- Gregory, W. K. 1933. Fish skulls: a study of the evolution of natural mechanisms. *Transactions of the American Philosophical Society* 23: 75-481.
- Günther, A. 1880. Report on the shore fishes procured during the voyage of H. M. S. "Challenger" in the years 1873-76. Report of the Scientific Results of the Voyage of H. M. S. Challenger during the Years 1873-76. *Zoology* 1(6): 1-82, pls. 1-32.
- Hallacher, L. E. 1974. The comparative morphology of the extrinsic gasbladder musculature in the scorpionfish genus *Sebastes* (Pisces: Scorpaeniformes). *Proceedings of the California Academy of Sciences* 15: 59-84.
- Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana, 263 pp.
- Herre, A. W. 1934. *Notes on fishes in the Zoological Museum of Stanford University. 1. The fishes of the Herre Philippine expedition of 1931*. The Newspaper Enterprise Ltd., Hong Kong, 106 pp.
- Hubbs, C. L. and Lagler, K. F. 1958. Fishes of the Great Lakes region. *Cranbrook Institute of Science Bulletin* 26: 1-213.
- Hureau, J. C. 1986. Platycephalidae. Pp. 1241-1242. In: P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen and E. Tortonese (eds). *Fishes of the north-eastern Atlantic and the Mediterranean*. Volume III. UNESCO, Paris.
- ICZN. 1985. *International code of zoological nomenclature*. 3rd ed. International Trust for Zoological Nomenclature, London. xx+338pp.
- Imamura, H. and Amaoka, K. 1994. A new species of flathead, *Grammoplites knappi* (Scorpaeniformes: Platycephalidae) from the South China Sea. *Japanese Journal of Ichthyology* 41: 173-179.
- Imamura, H. and Amaoka, K. 1996. *Rogadius serratus* (Cuvier, 1829), a senior synonym of *R. polijodon* (Bleeker, 1853) (Scorpaeniformes: Platycephalidae). *Ichthyological Research* 43: 97-100.
- Imamura, H., Ida, H. and Moyer, J. T. 1995. Redescription of a flathead, *Thysanophrys otaitensis* (Scorpaeniformes: Platycephalidae). *Japanese Journal of Ichthyology* 42: 287-293.
- Imamura, H. and Yabe, M. 1996. Larval record of a red firefish, *Pterois volitans* from northwestern Australia (Pisces: Scorpaeniformes). *Bulletin of the Faculty of Fisheries, Hokkaido University* 47: 41-46.
- Imamura, H., Yabe, M., Iguchi, M. and Amaoka, K. 1996. Juvenile development of a flathead, *Suggrundus meerdervoortii* (Scorpaeniformes: Platycephalidae). *Ichthyological Research* 43: 47-53.
- Imamura, H. and Knapp, L. W. 1997. A new species of deepwater flathead, *Bembras adenensis* (Scorpaeniformes: Bembridae) from the western Indian Ocean. *Ichthyological Research* 44.

(In press.)

- Ishida, M. 1994. Phylogeny of the suborder Scorpaenoidei (Pisces: Scorpaeniformes). Bulletin of Nansei National Fisheries Research Institute 27: 1-112.
- Johnson, G. D. 1980. The limits and relationships of the Lutjanidae and associated families. Bulletin of the Scripps Institution of Oceanography, University of California 24: 1-114.
- Johnson, G. D. 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and interrelationships of the Serranidae. Copeia 1983: 777-787.
- Johnson, G. D. 1984. Percoidei: development and relationships. Pp. 438-447. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson (eds). *Ontogeny and Systematics of Fishes*. Special Publication 1. American Society of Ichthyologists and Herpetologists, Lawrence.
- Johnson, G. D. and Fritzsche, R. A. 1989. *Graus nigra*, an omnivorous girellid, with a comparative osteology and comments on relationships of the Girellidae. Proceedings of the Academy of Natural Sciences of Philadelphia 141: 1-27.
- Johnson, G. D. and Patterson, C. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52: 554-626.
- Jordan, D. S. and Hubbs, C. L. 1925. Record of fishes obtained by David Starr Jordan in Japan. Memoirs of the Carnegie Museum 10: 93-346.
- Jordan, D. S. and Richardson, R. E. 1908. A review of the flatheads, gurnards and other mail-cheeked fishes from the waters of Japan. Proceedings of the United States National Museum 33: 629-670.
- Jordan, D. S. and Seale, A. 1905. List of fishes collected at Hong Kong by Captain William Finch, with description of five new species. Proceedings of the Davenport Academy of Sciences 10: 1-17.
- Jordan, D. S. and Seale, A. 1907. Fishes of the islands of Luzon and Panay. Bulletin of the Bureau of Fisheries 26: 1-48.
- Jordan, D. S. and Snyder, J. O. 1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States steamer Albatross, with descriptions of fourteen new species. Proceedings of the United States National Museum 23: 335-385.
- Jordan, D. S. and Thompson, W. F. 1913. Notes on a collection of fishes from the Island of Shikoku in Japan, with a description of a new species *Gnathypops iyonis*. Proceedings of the United State National Museum 46: 65-72.
- Kanayama, T. 1991. Taxonomy and phylogeny of the family Agonidae (Pisces: Scorpaeniformes). Memoirs of the Faculty of Fisheries, Hokkaido University 38: 1-199.
- Katayama, M. 1959. Study on the serranid fishes of Japan (I). Bulletin of the Faculty of Education, Yamaguchi University 6: 133-140.
- Keenan, C. P. 1991. Phylogeny of Australian species of flatheads (Teleostei, Platycephalidae) as determined by allozyme electrophoresis. Journal of Fish Biology 39: 237-249.
- Kido, K. 1988. Phylogeny of the family Liparididae, with the taxonomy of the species found around Japan. Memoirs of the Faculty of Fisheries, Hokkaido University 35: 125-256.
- Knapp, L. W. 1973. *Platycephalus beauforti*, a new species of flathead (Pisces, Platycephalidae) from the western Pacific. Proceedings of the Biological Society of Washington 86: 117-126.
- Knapp, L. W. 1979. Fische des Indischen Ozeans. Ergebnisse der ichthyologischen Untersuchungen während der Expedition des Forschungsschiffes 'Meteor' in den Indischen Ozean, Oktober 1964 bis 1965. A. Systematischer Teil, 22. Scorpaeniformes (4). Meteor Forschungsergebnisse. Reihe D 29: 48-54.
- Knapp, L. W. 1981. Platycephalidae. Pages 2pp. In: W. Fischer, G. Bianchi and W. B. Scott (eds). *FAO species identification sheets for fishery purposes. Eastern central Atlantic (Fishing Area 34*

- and part of 47). Vol. 3. FAO, Rome.
- Knapp, L. W. 1984. Platycephalidae. Pages 22pp. *In*: W. Fischer and G. Bianchi (eds). *FAO species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51)*. Vol. 3. FAO, Rome.
- Knapp, L. W. 1986. Family No. 155: Platycephalidae. Pp. 482-486. *In*: M. M. Smith and P. C. Heemstra (eds). *Smiths' sea fishes*. Springer-Verlag, Berlin.
- Knapp, L. W. 1987. New Australian fishes. Part 13. Two new species of Platycephalidae. *Memoirs of the Museum of Victoria* 48: 53-55.
- Knapp, L. W. 1991. *Platycephalus chauliodous*, a new flathead fish from the eastern Indian Ocean (Teleostei: Platycephalidae). *Proceedings of the Biological Society of Washington* 104: 23-29.
- Knapp, L. W. 1992. Status of type specimens of *Platycephalus rodericensis* Cuvier, 1829 and *P. borboniensis* Cuvier, 1829 (Pisces: Platycephalidae). *Proceedings of the Biological Society of Washington* 105: 389-392.
- Knapp, L. W. 1996. Review of the genus *Cociella* Whitley (Teleostei: Platycephalidae) with the description of three species. *Proceedings of the Biological Society of Washington* 109: 17-33.
- Knapp, L. W. and Wongratana, T. 1987. *Sorsogona melanopectera*, a new flathead fish from the northern Indian Ocean (Teleostei: Platycephalidae). *Proceedings of the Biological Society of Washington* 100: 381-385.
- Kojima, J. 1988. Scorpaenidae. Pp. 777-810. *In*: M. Okiyama (ed.). *An atlas of the early stage fishes in Japan*. Tokai University Press, Tokyo. (In Japanese.)
- Kusaka, T. 1974. *The urohyal of fishes*. University of Tokyo Press, Tokyo, xiv + 320 pp.
- Lacépède, B. G. E. 1880. *Histoire naturelle des poissons*. 2. C. F. G. Levrault, Paris-Strasbourg, lxiv + 632 pp., 20 pls.
- Lauder, G. V. and Liem, K. L. 1983. The evolution and interrelationships of the actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology* 150: 95-197.
- Leviton, A. E., Gibbs, Jr., R. H., Heal, E. and Dawson, C. E. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985: 802-832.
- Liem, K. F. 1970. Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Fieldiana: Zoology* 56: 1-166.
- Maddison, W. P., Donoghue, M. J. and Maddison, D. R. 1984. Outgroup analysis and parsimony. *Systematic Zoology* 33: 83-103.
- Matsubara, K. 1943. Studies on the scorpaenoid fishes of Japan: anatomy, phylogeny and taxonomy (I). *The Transactions of the Shigenkagaku Kenkyusho* 1: 1-170.
- Matsubara, K. 1955. *Fish morphology and hierarchy*. Ishizaki Shoten, Tokyo, xi + v + 1605 + viii pp., 135 pls. (In Japanese.)
- Matsubara, K. and Ochiai, A. 1955. A revision of the Japanese fishes of the family Platycephalidae (the flatheads). *Memoirs of the College of Agriculture, Kyoto University* (68): 1-109.
- McCulloch, A. R. 1914. Report on some fishes obtained by the F.I.S. "Endeavour" on the coasts of Queensland, New South Wales, Victoria, Tasmania, south and south-western Australia. Part II. Zoological Results of the Fishing Experiments Carried on by F.I.S. "Endeavour," 1909-1914 2: 75-165.
- McCulloch, A. R. 1927. The fishes and fish-like animals of New South Wales. Royal Zoological Society of New South Wales, Sydney, 104 pp., 43 pls.
- Mooi, R. D. 1993. Phylogeny of the Plesiopidae (Pisces: Perciformes) with evidence for the inclusion of the Acanthoclinidae. *Bulletin of Marine Science* 52: 284-326.

- Moser, H. G. and Ahlstrom, E. H. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California. *Journal of the Fisheries Research Board of Canada* 35: 981-996.
- Myers, R. F. 1989. *Micronesian reef fishes. A practical guide to the identification of the inshore marine fishes of the tropical central and western Pacific*. Coral Graphics, Guam, vi+298 pp.
- Nakabo, T. 1993. Platycephalidae. Pp. 535-539, 1299-1300. *In*: T. Nakabo (ed.). *Fishes of Japan with pictorial keys to the species*. Tokai University Press, Tokyo. (In Japanese.)
- Nelson, J. S. 1976. *Fishes of the world*. John Wiley and Sons, New York, xiii+373 pp.
- Nelson, J. S. 1984. *Fishes of the world. 2nd ed.* John Wiley and Sons, New York, xv+475 pp.
- Nelson, J. S. 1994. *Fishes of the world. 3rd ed.* John Wiley and Sons, New York, xvii+600 pp.
- Nursall, J. R. 1963. The caudal musculature of *Hoplopagrus guntheri* Gill (Perciformes: Lutjanidae). *Canadian Journal of Zoology* 41: 865-880.
- Ochiai, A. 1984. Platycephalidae. Pp. 321-322. *In*: H. Masuda, K. Amaoka, C. Araga, T. Uyeno and T. Yoshino (eds). *The fishes of the Japanese Archipelago*. English text. Tokai University Press, Tokyo.
- Ogilby, J. O. 1898. New genera and species of fishes. *Proceedings of the Linnean Society of New South Wales* 23: 32-41.
- Ogilby, J. O. 1910. On some new fishes from the Queensland coast. *Proceedings of the Royal Society of Queensland* 23: 85-139.
- Osse, J. W. M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Netherlands Journal of Zoology* 19: 289-392.
- Patterson, C. and Johnson, G. D. 1995. The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* (559): i-iv+1-85.
- Paxton, J. R., Hoese, D. F., Allen, G. R. and Hanley, J. E. 1989. *Zoological Catalogue of Australia. Vol. 7. Pisces. Petromyzonidae to Carangidae*. Australian Government Publishing Service, Canberra, xii+664 pp.
- Potthoff, T., Kelley, S., Moe, M. and Young, F. 1984. Description of porkfish larvae (*Anisotremus verginicus*, Haemulidae) and their osteological development. *Bulletin of Marine Science* 34: 21-59.
- Quast, J. C. 1965. Osteological characteristics and affinities of the hexagrammid fishes with a synopsis. *Proceedings of the California Academy of Sciences* 31: 563-600.
- Regan, C. T. 1913. The osteology and classification of the teleostean fishes of the order Scleroparei. *Annals and Magazine of Natural History. Series 8* 11: 169-184.
- Richardson, J. 1848. Ichthyology. Pp. 75-139, pls. 42-43, 44 (parts), 45-52, 53 (part). *In*: J. Richardson and J. E. Gray (eds). *The zoology of the voyage of H.M.S. Erebus and Terror under the command of Captain Sir James Clark Ross, R. N., F.R.S., during the years 1839-43*. Janson and Sons, London.
- Sainsbury, K. J., Kailola, P. J. and Leyland, G. G. 1985. *Continental shelf fishes of northern and north-western Australia*. Clouston and Hall and Peter Pownall Fisheries Information Service, Canberra, vii+375 pp.
- Sakashita, M. 1992. Taxonomic study of *Platycephalus indicus*-complex found in the western Pacific Ocean and the eastern Indian Ocean (Pisces: Platycephalidae). M.S. thesis, University of the Ryukyus, iv+42 pp.
- Sasaki, K. 1989. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the Faculty of Fisheries, Hokkaido University* 36: 1-137.
- Schultz, L. P. 1966. Platycephalidae. Pp. 45-62. *In*: L. P. Schultz and collaborators. *Fishes of the Marshall and Marianas Islands*. *Bulletin of the United States National Museum* 202.
- Scott, T. D., Glover, C. J. M. and Southcott, R. V. 1980. *The marine and freshwater fishes of South*

- Australia (second edition)*. D. J. Woolman, Government Printer, South Australia, 392 pp.
- Shao, K. T. and Chen, J. P. 1987. Fishes of the family Platycephalidae (Teleostei: Platycephaloidei) of Taiwan with descriptions of two new species. *Bulletin of the Institute of Zoology, Academia Sinica* 26: 77-94.
- Shao, K. T. and Chen, J. P. 1993. Platycephalidae. Pp. 255-260. *In*: S. C. Shen (ed.). *Fishes of Taiwan*. Department of Zoology, Natural Taiwan University, Taipei.
- Shinohara, G. 1994. Comparative morphology and phylogeny of the suborder Hexagrammoidei and related taxa (Pisces: Scorpaeniformes). *Memoirs of the Faculty of Fisheries, Hokkaido University* 41: 1-97.
- Steindachner, F. 1884. Ichthyologische Beiträge (13). 1. Beiträge zur Kenntniss der Fische Australiens. *Sitzungsberichte der Akademie der Wissenschaften Wien* 88: 1065-1108, pls. 1-8.
- Stiassny, M. L. J. 1981. The phyletic status of the family Cichlidae (Pisces: Perciformes): a comparative anatomical investigation. *Netherlands Journal of Zoology* 31: 275-314.
- Stiassny, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. *Journal of Zoology, London (B)* 1: 411-460.
- Stiassny, M. L. J. and Jensen, J. S. 1987. Labroid interrelationships revisited: Morphological complexity, key innovations, and the study of comparative diversity. *Bulletin of the Museum of Comparative Zoology* 151: 269-319.
- Swofford, D. L. 1991. *PAUP: phylogenetic analysis using parsimony. Version 3.0s*. Illinois Natural History Survey, Champaign.
- Tominaga, Y. 1968. Internal morphology, mutual relationships and systematic positions of the fishes belonging to the family Pemphelidae. *Japanese Journal of Ichthyology* 15: 43-95.
- Vari, R. P. 1978. The terapon perches (Percoidei, Teraponidae): a cladistic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* 159: 175-340.
- Waite, E. R. 1921. Illustrated catalogue of the fishes of South Australia. *Records of the South Australian Museum* 2: 1-208.
- Washington, B. B., Eschmeyer, W. N. and Howe, K. M. 1984. Scorpaeniformes: relationships. Pp. 438-447. *In*: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson (eds). *Ontogeny and Systematics of Fishes*. Special Publication 1. American Society of Ichthyologists and Herpetologists, Lawrence.
- Watrous, L. E. and Wheeler, Q. D. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30: 1-11.
- Whitley, G. P. 1930. Ichthyological miscellanea. *Memoirs of the Queensland Museum* 10: 8-31.
- Whitley, G. P. 1931a. Studies in ichthyology. No. 5. *Records of the Australian Museum* 18: 138-160.
- Whitley, G. P. 1931b. New names for Australian fishes. *Australian Zoologist*, 6: 311-334, 3 pls.
- Whitley, G. P. 1933. Studies in ichthyology. No. 7. *Records of the Australian Museum* 19: 60-112.
- Whitley, G. P. 1935. Studies in ichthyology. No. 9. *Records of the Australian Museum* 19: 215-250.
- Whitley, G. P. 1940. The Nomenclator Zoologicus and some new fish names. *Australian Naturalist* 1940: 241-243.
- Whitley, G. P. 1952. Some noteworthy fishes from Australia. *Proceedings of the Royal Zoological Society of New South Wales* 1950-51: 27-32.
- Wiley, E. O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. John Wiley and Sons, New York, xv + 439 pp.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia* 125: 225-317.

- Winterbottom, R. 1993. Search for the gobioid sister group (Actinopterygii: Percomorpha). *Bulletin of Marine Science* 52: 395-414.
- Yabe, M. 1985. Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. *Memoirs of the Faculty of Fisheries, Hokkaido University* 32: 1-130.
- Yabe, M. 1991. *Bolinia euryptera*, a new genus and species of sculpin (Scorpaeniformes: Cottidae) from the Bering Sea. *Copeia* 1991: 329-339.
- Yabe, M. and Uyeno, T. 1996. Anatomical description of *Normanichthys crockeri* (Scorpaeniformes, *incertae sedis*: family Normanichthyidae). *Bulletin of Marine Science* 58: 494-510.

Appendices

Appendix 1. List of the transformation series (TS) and characters used in the first-step analysis.

TS 1. Fifth infraorbital. 0: firmly attached to sphenotic; 1: fused to sphenotic. Fusion is apomorphic, because such does not occur between the fifth infraorbital and sphenotic in percoids (Katayama 1959; Fraser 1968, 1972; Tominaga 1968; Sasaki 1989; pers. obs.).

Remarks. Although Ishida (1994) recognized the latter condition as absence of the fifth infraorbital in the scorpaenid *Iracundus*, as well as in setarchids, tetraogids, synanceiids, gnathanacanthids, aploactids, congiopodids and pataecids, it was apparent that fusion has occurred between the infraorbital and sphenotic, because species of the above groups examined in this study have a tubular structure, which is usually found on the fifth infraorbital, rather than the sphenotic in other scorpaenoids.

TS 2. Sensory canal between circumorbital bones and neurocranium. 0: present; 1: absent. Absence of the canal is considered apomorphic, owing to its presence between the second infraorbital and neurocranium in percoids (Branson and Moore 1962; pers. obs.).

TS 3. Lachrymal and second infraorbital. 0: separated by first infraorbital; 1: attached; 2: separated by first infraorbital and ectopterygoid. Both the articulation of the lachrymal and second infraorbital and their separation by the first infraorbital and ectopterygoid are apomorphic characters, neither condition being found in percoids (Katayama 1959; Fraser 1968, 1972; Tominaga 1968; Sasaki 1989; pers. obs.) (unordered).

TS 4. Second and fourth infraorbitals. 0: separated by third infraorbital; 1: attached. Attachment of the second and fourth infraorbitals is apomorphic, since they are separated by the third infraorbital in percoids (Katayama 1959; Fraser 1968, 1972; Tominaga 1968; Sasaki 1989; pers. obs.).

TS 5. Second infraorbital and lateral ethmoid. 0: separated; 1: attached. The second infraorbital and lateral ethmoid are not attached in percoids (Katayama 1959; Fraser 1968, 1972; Tominaga 1968; Sasaki 1989; pers. obs.), such being the primitive character.

TS 6. Direction of opening of second infraorbital, continuous with sensory canal of third to fifth infraorbitals. 0: upward; 1: backward. A backwardly-directed opening is

apomorphic, since percoids have an upward opening only (Katayama 1959; Fraser 1968, 1972; Tominaga 1968; Sasaki 1989; pers. obs.).

TS 7. Tubercles on head. 0: absent; 1: present. Tubercles are usually absent from the head in percoids (Tominaga 1968; Fraser 1972; Vari 1978; Sasaki 1989; pers. obs.). Accordingly, their presence is apomorphic.

TS 8. Number of tooth plates on prevomer. 0: one; 1: two; 2: absent. Two plates on the prevomer and plates absent are both regarded as apomorphic, because a single tooth plate only found in percoids (Fraser 1968; Sasaki 1989; pers. obs.) (unordered).

TS 9. Lateral opening on pterotic continuous with preopercle. 0: absent; 1: present. A lateral opening of the sensory canal on the pterotic is usually absent in percoids (Fraser 1968; Tominaga 1968; pers. obs.). Accordingly, the presence of an opening is regarded as apomorphic.

TS 10. Baudelot's ligament. 0: originating from the basioccipital; 1: originating from the first vertebra; 2: absent. Percoids usually have Baudelot's ligament originating from the basioccipital (Gosline 1966; Sasaki 1989; Mooi 1993; pers. obs.). Accordingly, conditions (1) and (2) are apomorphic (unordered).

TS 11. Prootic and intercalar. 0: articulated; 1: separated. Separation of the prootic and intercalar is apomorphic, because they are articulated to each other in percoids (Fraser 1968; Tominaga 1968; Sasaki 1989; pers. obs.).

TS 12. Sensory canal between pterotic and preopercle. 0: present; 1: absent. Absence of the canal is regarded as apomorphic, since it is present in percoids (Branson and Moore 1968; pers. obs.).

TS 13. Nasal and neurocranium. 0: loosely articulated; 1: sutured. The nasal sutured to the neurocranium is regarded as apomorphic, because the former is always loosely articulated in percoids (Fraser 1968; Tominaga 1968; Sasaki 1989; pers. obs.).

TS 14. Nasals. 0: separated; 1: sutured medially. The nasals are separated in percoids (Fraser 1968; Tominaga 1968; Sasaki 1989; pers. obs.). Accordingly, the sutured condition is considered apomorphic.

TS 15. Lateral ethmoids. 0: separated; 1: meeting in midline. The lateral ethmoids are separated in percoids (e. g. Katayama 1959; Fraser 1968, 1972; Tominaga 1968; Sasaki 1989; pers. obs.). Therefore, their meeting in the midline is apomorphic.

TS 16. Ascending process of premaxillary. 0: continuous with remaining part of premaxillary; 1: separated. The process is usually continuous with the remaining part of the premaxillary in percoids (Fraser 1968; Tominaga 1968; Vari 1978; Sasaki 1989; pers. obs.). Therefore, separation is apomorphic.

TS 17. Notch between ascending process and cranial condyle. 0: present; 1: absent. A notch between the ascending process and cranial condyle is present in percoids (Fraser 1968; Tominaga 1968; Vari 1978; Sasaki 1989; pers. obs.). Accordingly, loss of the notch is considered apomorphic.

TS 18. Teeth on jaws. 0: present; 1: absent. Absence of jaw teeth, which are usually present in percoids, is regarded as apomorphic (Tominaga 1968; Liem 1970; Sasaki 1989; pers. obs.).

TS 19. Teeth on palatine. 0: present; 1: absent. Percoids typically have small canines on the palatine (Fraser 1968; Tominaga 1968; Johnson 1980; pers. obs.). Therefore, absence of teeth is apomorphic.

TS 20. Metapterygoid lamina. 0: present; 1: absent. A lamina is usually present in percoids; its absence is therefore regarded as apomorphic (Johnson 1980; Sasaki 1989; pers. obs.).

TS 21. Entopterygoid. 0: large; 1: small; 2: absent. Percoids have a large, oval entopterygoid (Katayama 1959; Tominaga 1968; Sasaki 1989; pers. obs.). Reduction in size and loss of this element are regarded as apomorphic (unordered).

TS 22. Backwardly-directed opercular spine. 0: absent; 1: present; 2: secondarily absent. The spine is present in all platycephaloids and scorpaenoids, except *Dendrochirus*, in which it has been lost secondarily. The spine is usually absent in percoids (Gosline 1966; Johnson 1983; pers. obs.). Therefore, the conditions (1) and (2) are apomorphic characters (ordered as 0-1-2).

TS 23. Urohyal and first basibranchial. 0: attached by ligament; 1: sutured. The urohyal and first basibranchial sutured is apomorphic, since this condition is not found in percoids (Sasaki 1989; pers. obs.).

TS 24. Basihyal. 0: ossified; 1: cartilaginous; 2: absent. Percoids have an ossified basihyal (Tominaga 1968; Stiassny and Jensen 1987; Sasaki 1989; pers. obs.). Both a cartilaginous basihyal and absence of that element are considered apomorphic (unordered).

TS 25. Hypohyals and basihyal. 0: not articulated; 1: articulated. The hypohyals and basihyal are not articulated with each other in percoids (pers. obs.). Articulation is therefore regarded as apomorphic.

TS 26. Interarcual cartilage. 0: present; 1: absent. The interarcual cartilage is usually present in percoids (Stiassny 1981; Stiassny and Jensen 1987; Sasaki 1989; pers. obs.). Hence absence of the cartilage is regarded as apomorphic.

Remarks. Ishida (1994) considered *Inimicus*, *Minous* and *Erisphex* to have an ossified interarcual cartilage, accompanied by loss of the second pharyngobranchial. Examination of the small second pharyngobranchial (without a tooth plate) and interarcual cartilage in *Hypodytes* suggested that Ishida's "ossified interarcual cartilage" is homologous with the second pharyngobranchial lacking a tooth plate and that an interarcual cartilage is absent in *Inimicus*, *Minous* and *Erisphex*.

TS 27. Tooth plate on third epibranchial. 0: present; 1: absent. Percoids have a tooth plate on the third epibranchial, absence of the plate therefore being apomorphic (Tominaga 1968; Sasaki 1989; pers. obs.).

TS 28. First pharyngobranchial. 0: ossified; 1: cartilaginous. Because percoids have an ossified first pharyngobranchial, a cartilaginous first pharyngobranchial is apomorphic (Stiassny and Jensen 1987; Sasaki 1989; pers. obs.).

TS 29. Tooth plate on second pharyngobranchial. 0: present; 1: absent. Absence of a tooth plate is apomorphic, since such is present in percoids (Tominaga 1968; Sasaki 1989; pers. obs.).

TS 30. Pharyngobranchials. 0: separated; 1: third and fourth fused; 2: second to fourth fused. Fusions of these bones represent apomorphies, because percoids have the pharyngobranchials separated (Tominaga 1968; Stiassny and Jensen 1987; Sasaki 1989; pers. obs.) (ordered as 0-1-2).

TS 31. Configuration of actinosts. 0: uppermost smallest, progressively longer ventrally; 1: short and broad; 2: rectangular. The upper actinost is smallest, and more ventral ones successively longer, in percoids (Katayama 1959; Gosline 1966; Tominaga 1968; Sasaki 1989; pers. obs.). Accordingly, both short and broad, and rectangular actinosts are apomorphic conditions (unordered).

TS 32. Cartilaginous band between scapula and coracoid. 0: narrow; 1: broad. The cartilaginous band between the scapula and coracoid is narrow in percoids (Gosline 1966; Tominaga 1968; Sasaki 1989; pers. obs.). Accordingly, a broad cartilaginous

band represents an apomorphy.

TS 33. Lower free ray(s) of pectoral fin. 0: absent; 1: present. Because free rays are usually absent in percoids (Yabe 1985; pers. obs.), their presence represents a derived condition.

TS 34. Uppermost actinost and scapula. 0: separated; 1: fused. Fusion is considered apomorphic, since the uppermost actinost is separated from the scapula in percoids (Katayama 1959; Gosline 1966; Tominaga 1968; Sasaki 1989; pers. obs.).

TS 35. Pectoral fin rays. 0: middle rays branched; 1: all rays unbranched. Branched rays are usually present in percoids (Ishida 1994; pers. obs.). Hence, a pectoral fin without branched rays is apomorphic.

TS 36. Posteromedial portion of pelvic bones. 0: articulated; 1: separated. Postmedial separation of the pelvic bones is apomorphic, since there is no such separation in percoids (Katayama 1959; Gosline 1966; Tominaga 1968; Sasaki 1989; Mooi 1993; pers. obs.).

TS 37. Posterior pelvic fossa. 0: absent; 1: present. Presence of a fossa is apomorphic because such is not usually seen in percoids (Katayama 1959; Gosline 1966; Fraser 1968; Tominaga 1968; Sasaki 1989; Mooi 1993; pers. obs.).

TS 38. Cartilaginous caps on anterior portion of pelvic bones. 0: separated; 1: fused. The cartilaginous caps on the anterior portion of the pelvic bones are separated in percoids (Mooi 1993; pers. obs.). Accordingly, fusion is considered apomorphic.

TS 39. Number of soft pelvic fin rays. 0: five; 1: four; 2: two. Four and two rays are apomorphic, because percoids have five soft rays (Nelson 1994; pers. obs.) (ordered as 0-1-2).

TS 40. First spine on first dorsal fin proximal pterygiophore. 0: present; 1: absent. Absence of the spine is apomorphic since it is usually present in percoids (Gosline 1966; Johnson 1983; Sasaki 1989; pers. obs.).

TS 41. First spine on first anal fin proximal pterygiophore. 0: present; 1: absent. Percoids have two spines on the first anal fin proximal pterygiophore (Sasaki 1989; Baldwin and Johnson 1993; pers. obs.). Absence of the spine is considered apomorphic.

TS 42. Second element on first anal fin proximal pterygiophore. 0: hard spine; 1: soft ray; 2: absent. The second element on the pterygiophore being a soft ray or lost entirely is apomorphic, since percoids usually have two spines on the first anal fin proximal pterygiophore (Sasaki 1989; Baldwin and Johnson 1993; pers. obs.) (unordered).

TS 43. Ray on second anal fin proximal pterygiophore. 0: spine; 1: soft ray. The second anal fin proximal pterygiophore supports a spine in percoids (pers. obs.). Accordingly, a soft ray on the pterygiophore is apomorphic.

TS 44. Dorsal spines. 0: stout; 1: slender. Percoids usually have stout dorsal spines (pers. obs.). Therefore, the slender dorsal spines are considered apomorphic.

TS 45. Stay. 0: ossified; 1: cartilaginous. An ossified stay is present in percoids, a cartilaginous stay being the apomorphic character (Johnson 1984; Sasaki 1989; pers. obs.).

TS 46. First and second neural spines. 0: straight; 1: bent anteriorly. The bent condition of the first and second neural spines is apomorphic, since they are straight in percoids (Johnson 1983; Sasaki 1989; Baldwin and Johnson 1993; pers. obs.).

TS 47. Soft dorsal and anal fin rays. 0: branched; 1: unbranched. The soft dorsal and anal fin rays are usually branched in percoids (Ishida 1994; pers. obs.).

Accordingly, the unbranched condition is apomorphic.

TS 48. Number of rays supported by posteriormost proximal pterygiophores. 0: two; 1: one. Two rays are usually supported by the posteriormost proximal pterygiophores in percoids (Johnson 1984; pers. obs.). A single ray is considered apomorphic.

TS 49. Dorsal fin proximal pterygiophores. 0: not exposed; 1: exposed along first dorsal fin; 2: exposed along both dorsal fins. Both conditions of exposure of the dorsal fin proximal pterygiophores are considered apomorphic, because neither occurs in percoids (pers. obs.) (ordered as 0-1-2).

TS 50. Urostyle. 0: separated from upper hypural complex; 1: fused to complex. The urostyle is separated from the hypurals in percoids (Tominaga 1968; Potthoff *et al.* 1984; Sasaki 1989; Fujita 1990; pers. obs.). Accordingly, fusion is considered apomorphic.

TS 51. Parhypural and hypural. 0: separated; 1: fused. These bones are usually separated in percoids (Tominaga 1968; Potthoff *et al.* 1984; Sasaki 1989; Fujita 1990; pers. obs.), their fusion being regarded here as apomorphic.

TS 52. Hemal spine and third preural centrum. 0: separated; 1: fused. The hemal spine is separated from preural centrum 3 in percoids (Tominaga 1968; Potthoff *et al.* 1984; Sasaki 1989; pers. obs.). Hence, fusion is considered apomorphic.

TS 53. Origin of levator operculi. 0: pterotic; 1: pterotic and posttemporal. The levator operculi usually originates from the pterotic only in percoids (Stiassny 1981; Sasaki 1989; pers. obs.). Therefore, its origin from both the pterotic and posttemporal is considered apomorphic.

TS 54. Insertion of sternohyoideus. 0: lateral aspects of urohyal; 1: lateral and ventral aspects of urohyal. Insertion onto both the lateral and ventral aspects of the urohyal is apomorphic, because the muscle is inserted only onto the lateral aspects in percoids (pers. obs.).

TS 55. Transversus dorsalis anterior. 0: branched; 1: unbranched. The unbranched condition is apomorphic because the transversus dorsalis anterior is usually branched in percoids (Stiassny and Jensen 1987; Sasaki 1989; pers. obs.).

TS 56. Levator posterior. 0: present; 1: absent. The muscle is present in percoids; absence is therefore regarded as apomorphic (Stiassny 1981; Stiassny and Jensen 1987; Sasaki 1989; pers. obs.).

TS 57. Transversus ventralis anterior and posterior. 0: overlapped; 1: separated. Separation of these muscles is considered to be the derived condition, since they overlap in percoids (Sasaki 1989; pers. obs.).

TS 58. Protractor pectoralis. 0: sheet-like muscle only; 1: comprised of sheet-like anterior and robust posterior elements. The occurrence of two elements is apomorphic, since such a condition is not seen in percoids (Greenwood and Lauder 1981; Sasaki 1989; pers. obs.).

TS 59. Muscle bundles serving free pectoral fin rays. 0: not separated from adjacent muscle; 1: separated. Separation is considered apomorphic because it is not seen in percoids (Sasaki 1989; pers. obs.).

TS 60. Division of bundles of adductor superficialis serving free pectoral fin rays. 0: absent; 1: present. Such a division is absent in percoids. Its presence is considered apomorphic (Sasaki 1989; pers. obs.).

TS 61. Adductor superficialis pelvici. 0: connected directly to pelvic fin rays; 1: connected to rays via a long strong tendon. The adductor superficialis pelvici is

connected directly to the pelvic fin rays in percoids (pers. obs.). Therefore, the existence of a tendon is apomorphic.

TS 62. Dorsal elements of pelvic fin muscles. 0: not attached to pectoral girdle; 1: attached to girdle. The dorsal elements of the pelvic fin muscles (adductor superficialis pelvici, adductor profundus pelvici and extensor proprius) are not attached to the pectoral girdle in percoids (pers. obs.). Therefore, attachment is considered apomorphic.

TS 63. Extensor proprius. 0: present; 1: absent. Absence of the muscle is apomorphic, since the extensor proprius is present in percoids (Liem 1970; Sasaki 1989; Shinohara 1994; pers. obs.).

TS 64. Flexor ventralis externus. 0: present; 1: absent. Absence of this muscle is apomorphic, since it is present in percoids (Nursall 1963; Sasaki 1989; pers. obs.).

TS 65. Obliquus superioris. 0: extending to neurocranium; 1: not extending to neurocranium. Failure of the obliquus superioris to extend to the neurocranium is regarded as apomorphic, since such an extension is present in percoids (pers. obs.).

TS 66. Extrinsic muscle. 0: absent; 1: present. Presence of the muscle is apomorphic, since it is usually absent in percoids (Sasaki 1989; pers. obs.).

TS 67. Intrinsic muscle. 0: absent; 1: present. Because the intrinsic muscle is usually absent in percoids (Vari 1978; Sasaki 1989; pers. obs.), its presence is considered apomorphic.

TS 68. Number of openings to exterior in lateral line scales. 0: one; 1: more than two. Percoids have a single backwardly-directed opening posteriorly on the lateral line scales (pers. obs.). More than two openings is considered apomorphic.

TS 69. Lateral line. 0: with scales; 1: with tube-like bones. The presence of tube-like bones in the lateral line is apomorphic, since such are not found in percoids (pers. obs.).

TS 70. Distinct spine on scales in lateral line. 0: absent on all scales; 1: a single spine present on all scales; 2: two spines present on all scales. All scales bearing one or two spines are considered apomorphic, since such conditions do not usually occur in percoids (pers. obs.) (ordered as 0-1-2).

TS 71. Bony plate-like lateral line scales. 0: absent; 1: present. Presence of bony plate-like lateral line scales is apomorphic, since such are not usually seen in percoids (Nelson 1994; pers. obs.).

TS 72. Body scales. 0: present; 1: absent, except on dorsal region; 2: entirely absent. Body scales are usually present in percoids (Nelson 1994; pers. obs.). Accordingly, characters (1) and (2) are apomorphic (ordered as 0-1-2).

TS 73. Bony plates on body. 0: absent; 1: present. Such plates are not usually found in percoids (Nelson 1994; pers. obs.), so their presence is apomorphic.

Appendix 2. Matrix of characters in transformation series used for first-step analysis.
0, primitive character; 1-2, derived characters.

Taxon	TRANSFORMATION SERIES						
	1-5	6-10	11-15	16-20	21-25	26-30	31-35
1. <i>Sebastes</i>	00000	00000	00000	00000	01000	00000	00010
2. <i>Sebastiscus</i>	00000	00000	00000	00000	01000	00000	00010
3. <i>Adelosebastes</i>	00000	00000	00000	00000	01000	00000	00010
4. <i>Hozukius</i>	00000	00000	00000	00000	01000	00000	00010
5. <i>Helicolenus</i>	00000	00000	00000	00000	01000	00000	00010
6. <i>Sebastolobus</i>	00000	00000	00000	00000	01000	00000	00000
7. <i>Dendrochirus</i>	01000	10000	00000	00010	02000	00000	00000
8. <i>Pontinus</i>	01000	10000	00000	00000	01000	00000	00001
9. <i>Scorpaena</i>	01000	10000	00000	00000	01000	00000	00010
10. <i>Scorpaenodes</i>	01000	10000	00000	00010	01000	00000	00000
11. <i>Scorpaenopsis</i>	11000	10000	00000	00010	01000	00000	00010
12. <i>Trachyscorpia</i>	01000	10000	00000	00000	01000	00000	00000
13. <i>Setarches</i>	11000	10000	00000	00000	01000	00000	00000
14. <i>Neosebastes</i>	00000	00000	00000	00000	01000	00000	00010
15. <i>Apistus</i>	10000	01000	00000	01001	01000	00000	00110
16. <i>Hypodytes</i>	10000	00000	00000	00001	01000	01010	00010
17. <i>Inimicus</i>	10000	00001	00000	00011	01000	11010	00110
18. <i>Minous</i>	10000	00101	00000	00011	01000	11011	00111
19. <i>Erisphex</i>	11000	00001	11000	00011	01000	11011	00011
20. <i>Plectrogenium</i>	10000	00000	01000	00000	01000	00000	00000
21. <i>Bembradium</i>	00000	00100	01000	00000	01000	10100	00000
22. <i>Parabembras</i>	00000	00000	00000	10000	01000	00000	10000
23. <i>Bembras</i>	00000	00000	00000	00000	01000	00000	10000
24. <i>Chelidonichthys</i>	00111	01010	00100	01010	11020	10000	21100
25. <i>Lepidotrigla</i>	00111	01110	10101	01010	11020	10000	21100
26. <i>Pterygotrigla</i>	00111	01211	00101	01010	11020	10000	21100
27. <i>Prionotus</i>	10111	01110	00100	01000	11000	10000	21100
28. <i>Bellator</i>	10111	01010	00101	01000	11000	10000	21100
29. <i>Peristedion</i>	00201	01211	10110	01110	11010	01001	21100
30. <i>Satyrichthys</i>	00201	01211	10110	01110	11010	11002	21100
31. <i>Hoplichthys gilberti</i>	10000	01001	11000	10001	21001	10110	21100
32. <i>H. langsdorfii</i>	10000	01002	11000	10001	21001	10110	21100
33. <i>H. haswelli</i>	10000	01001	11000	10001	21001	10110	21100
34. <i>Platycephalidae</i>	00000	00010	00000	10000	01100	00000	10000

Appendix 2. Continued.

TRANSFORMATION SERIES								
	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-73
1.	00000	00000	00000	00000	00000	00000	10000	000
2.	00000	00000	00000	00000	00000	00000	10000	000
3.	00000	00000	00000	00000	00000	00000	10000	000
4.	00000	00000	00000	00000	00000	00000	10000	000
5.	00000	00000	00000	00000	00000	00000	10000	000
6.	00000	00000	00000	00000	00000	00000	10000	000
7.	00000	00000	00000	00100	00000	00000	10000	000
8.	00000	00000	00000	00000	00000	00000	10000	000
9.	00000	00000	00000	00000	00000	00000	10000	000
10.	00000	00000	00000	00000	00000	00000	10000	000
11.	00000	00000	00000	00000	00000	00000	10000	000
12.	00000	00000	00000	00000	00000	00000	10000	000
13.	00000	00000	00000	00000	00000	00000	10000	000
14.	00000	00000	10000	00000	00000	00000	10000	000
15.	00000	00000	10000	10101	00000	00000	11000	000
16.	00010	00000	10000	10100	00000	00000	10010	000
17.	00000	00100	10101	11101	00000	00000	10010	020
18.	00001	00100	11101	11101	00000	00000	10010	020
19.	00020	10000	11101	11101	00000	00100	10010	000
20.	01000	00001	00000	00001	00000	00000	10000	000
21.	01000	12101	00000	00001	10000	00000	10000	000
22.	01000	00000	00000	00000	00000	00000	10000	000
23.	01000	11100	00000	00000	00000	00000	10000	000
24.	01101	11100	00021	00001	01011	01010	01100	000
25.	01001	11100	00021	00001	01011	01010	01100	000
26.	01001	11100	00011	00001	01011	01011	10000	000
27.	01100	11100	00000	00001	01011	01010	01000	000
28.	01100	11100	00000	00001	01011	01010	11000	000
29.	11101	11110	00001	11001	01011	01001	10001	101
30.	01101	11110	00001	11001	01011	01001	10001	101
31.	11101	11110	00001	11001	10100	01000	10001	120
32.	11101	11110	00001	11001	10100	01001	10002	120
33.	11101	11110	00001	11001	10000	00001	10001	110
34.	11001	12100	00000	00011	00100	10000	10100	000